Apportionment of Genetic Variation in Contemporary Aleut and Eskimo Populations of Alaska Using Anthropometrics and Classical Genetic Markers

By

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ABSTRACT

This thesis attempts to answer: 1) How has history and evolution shaped the relationship of Aleut and Eskimo populations? and 2) What is the relationship of Aleuts and Eskimos to other Native American populations? Questions are addressed using anthropometric measurements and classical genetic markers. Relethford-Blangero method was applied to athropometrics of the study populations. Results were compared to Nei's genetic distance matrix of classical genetic markers. Multivariate analyses were used to determine relationships among Aleuts, Eskimos and other American Indians. This study shows a close phylogenetic relationship among Aleuts and Eskimos. Anthropometrics reveal a close relationship between Savoonga, Gambell and St. Paul due to shared European admixture. Despite shared population history, St. George did not cluster with the other Bering Sea natives in the PCA, NJT, or unscaled R-matrices; highlighting affects of genetic drift on St. George. A close relationship between Aleuts, Eskimos, Northwest, and Northeast Natives was evident.

This thesis is dedicated to the memory of my mother, Anne Michele Guthier Justice. She was my inspiration, motivation, and her sacrifices for this work were as great as my own.

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CHAPTER 1: INTRODUCTION

Anthropometrics were widely utilized primarily for the purposes of racial classification at the turn of the 20th century. Many older data sets for anthropometrics are incomparable due to absence of measurement of inter-observer error in, no consensus on how to pool populations, or absence of age of individual on data sheets (Johnston and Schell 1979). Around the same time, several large expeditions were undertaken to collect measurements across the Americas, including the World's Columbian Exposition, Jesup North Pacific Expedition, and the Huntington California Expedition. The large data sets that resulted from these expositions defied detailed analysis due to the absence of computer technology and programs to properly analyze the data beyond basic description. Boas, aware of these difficulties and the confounding effects of inter-observer error, set forth to consolidate measurements on North American natives. He organized a team of more than 50 anthropologists, most of who were trained by him personally to accomplish the task (Jantz 2006).

However, since Boas' seminal work at the turn of the 20th century with American immigrants, most anthropologists have been under the impression that the plasticity of human physical characteristics was so great that it would obscure the detection of microevolution through analysis of anthropometrics (Madrigal et al 2003, Jantz 2006). Interest in anthropometrics as a means of studying population phylogeny and structure waned, while the use of classical genetic and then molecular markers increased. With the development of computers and the availability of multivariate

statistics, methodologies specific to these new markers, were developed and implemented. These new methods of analysis led biological anthropology away from being a descriptive science to a greater emphasis on the processes of evolutionary forces acting upon humans.

Well into the 1970s, some anthropologists continued to characterize populations and describe the differences among shape, size, and qualitative characteristics between groups. In an attempt to reject the concept of "race" anthropologists adhered to Boas' findings that these traits were too ecosensitive and could easily change under selective pressure in just one generation. In the late 1960s and 1970s and into the new millennium, researchers began utilizing new multivariate techniques, not available to Boas, with which to apply anthropometrics to questions of human evolution and genetic structure (Lees and Crawford 1976, Relethford et al 1980). Multivariate statistics have now challenged Boas' original claims concerning the plasticity of anthropometric traits. Studies have shown that craniometric traits are influenced by environmental plasticity, but not to the degree that was originally claimed by Boas. Therefore, this plasticity does not obscure overall relationships among populations due to geography and population history (Sparks and Jantz 2002, Gravlee et al 2003, Relethford 2004).

Recent studies of both living and ancient populations have indicated that anthropometrics, much like genetic markers, can be applied to the study of microevolutionary forces acting on human groups (Relethford et al 1980, Relethford and Blangero 1990, Relethford et al 1997, Relethford 1996, Relethford et al 1997,

Relethford and Harpending 1994, Scherer 2007, Williams-Blangero and Blangero 1989, Gonzalez-Jose et al 2007). Although anthropometric traits are affected by environmental factors, some have high heritabilities and adequately reflect the phylogenetic histories of populations (Devor et al 1986a, Devor et al 1986b).

A goal of this thesis is to determine the efficacy of anthropometric measurements (collected on the Aleut and Eskimo populations of the Bering Sea) in inferring population history and substructure. To do this, the thesis will answer the following: 1) How has history and evolution shaped the relationship of Aleut and Eskimo populations residing in the Bering Sea? 2) What is the relationship of Aleuts and Eskimos to other Native American populations? 3) How do relationships among arctic populations based on anthropometrics compare to phylogenies based on Mendelian markers?

St. Paul and St. George islands (See Figure 1) house communities that were transplanted to the Pribilofs from the islands of Unmak and Unalaska in the Eastern Aleutian archipelago. Because of the location of fur seal breeding grounds, they were moved here by the Russians from 1823-1826 in order to hunt fur seals for pelts (Black 1983). In 1867, the US purchased Alaska from Russia, including Aleutian and Pribilof Islands. During WWII, the Japanese invaded Attu and Kiska, and the Aleuts were evacuated to Alaska. In 1942, the Pribilovians were moved to Funter Bay west of Juneau, Alaska (Lantus 1984). By 1945 St. Paul and St. George were resettled. (Kolhoff 1995). St. Paul's population began to grow after resettlement, in part due to the immigration of non-natives to the islands as workers in the crabbing industry. The

1970 census reveals that there were 428 natives and 22 non-natives residing on St. Paul, while there were only 156 natives and 7 non-natives on St. George (Lantis 1984).

Unlike St. Paul and St. George, the Eskimos have a long history of occupation on the island of St. Lawrence. Given their shared Yupik language and close geographical proximity to Siberia, the St. Lawrence Eskimos had strong cultural ties to Siberians, despite their political affiliation with the United States (Byard 1981). Following European contact, there was a great reduction in the population size on the island due to disease and depletion of resources, costing St. Lawrence nearly two thirds of its population (Hughes 1984, Byard and Crawford 1991). Then in 1900, the US government attempted to rebuild the Eskimo community by introducing reindeer herds and herders to help transition the Eskimos from maritime and hunting subsistence patterns to herding (Hughes 1984). It was the younger families of Gambell that left to follow the herds to a better grazing ground (Hughes 1984, Byard and Crawford 1991). The herd finally stopped in an area about 40 miles to the east of Gambell, where Savoonga is currently situated (See Figure 1) (Byard and Crawford 1991). The 1920s brought economic and health relief to St. Lawrence allowing for a population recovery (Hughes 1984). Population growth was greatest in Savoonga rather than Gambell. The population growth in Savoonga was principally facilitated by a larger breeding population, as the younger generation founded the new settlement representing a higher proportion of the total population than did Gambell's (Byard and Crawford 1991).

Anthropometric measurements will be utilized to elucidate the relationship between the Aleuts and Eskimos of the Bering Sea. In 1979 William S. Laughlin measured Eskimo populations from St. Lawrence Island, followed by Aleuts from the Pribilofs Islands in 1981. Additionally, blood group markers are compiled from the literature to compare relationships inferred from genetics and those from anthropometrics.

To understand the relationships among North American native populations, multivariate statistics are applied to data compiled from the literature as well as data collected by Boas' team of anthropometrists around the turn of the 20th century. Northern North American natives were measured by Boas and a team of trained anthropometrists from 1890 to 1904 (Jantz 2006, Jantz 1995, Jantz et al 1992). Measurements of Middle Americans were collected across a large span of time, ranging from 1898 until 1952. Caution must be exercised when interpreting relationships and ethnohistory based on such a heterogeneous sample. However, it is important to reexamine older data sets to determine if any patterns between geography and anthropometrics can be ascertained. Also, these results can be compared to studies based on genetics to elucidate their worth.

The following chapters contain a summary of the history and demography of populations, their analyses, and results related to this study. Chapter two highlights the history, archaeology, and biology of the Aleuts of the Pribilofs Islands and Eskimos of St. Lawrence Islands. Chapters three and four outline the materials and

analytical methods utilized for this study. Chapter five provides the results of all analyses. Finally, chapter six offers discussion and conclusions based on the data.

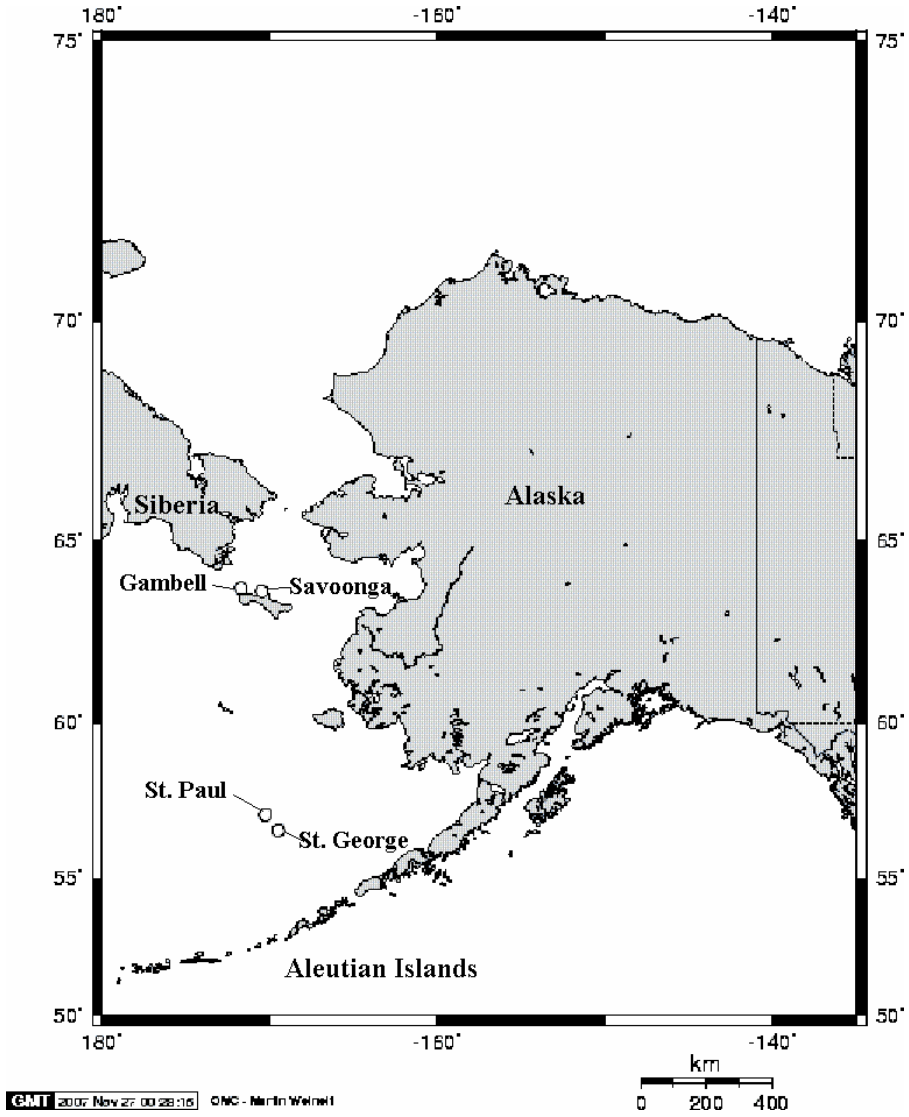


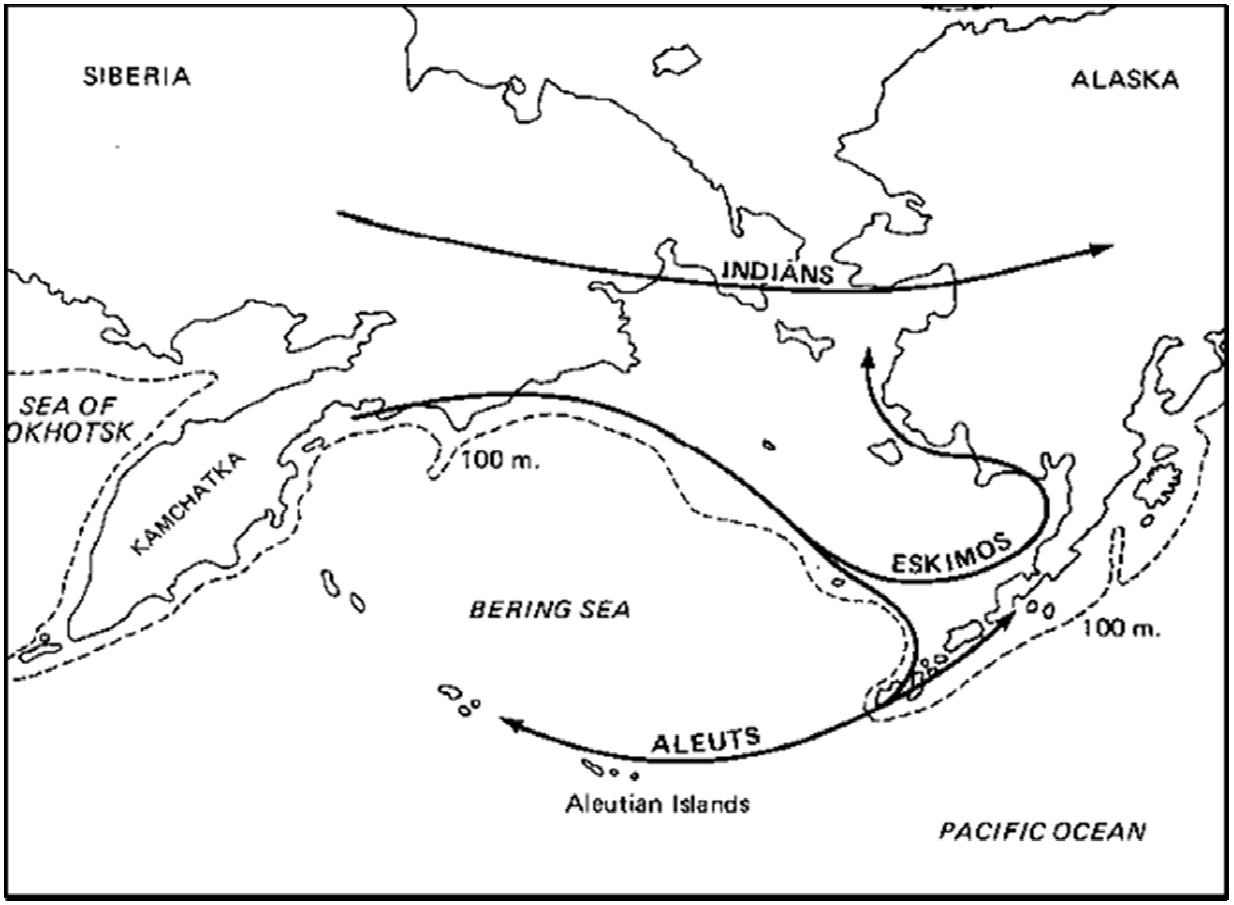
Figure 1. Map of eastern Bering Sea highlighting the locations of St. Lawrence Island Eskimo communities of Gambell and Savoonga, and Aleut communities of St. Paul and St. George. Map created using Online Mapping Creation (Weinelt 1996).

CHAPTER 2: LITERATURE REVIEW

Laughlin and Harper (1979) have proposed, based on linguistic, cultural, craniometric and genetic evidence, that Aleut and Eskimo populations share recent common ancestry (See Figure 2 for migration path of recent common ancestor). Aleut and Eskimo languages belong to the same language family (Eskimo-Aleut), which, based on glottochronology estimates, diverged between 5,000 and 11,000 years ago (Greenberg et al. 1985). Both groups traditionally relied on open-sea hunting technology and sea mammals for their subsistence, used rain-resistant gut clothing, and shared other technology and cultural items (Laughlin 1980). The Aleuts and Eskimos are similar in appearance, have relatively high sitting heights, medium to sub-medium stature, and small hands and feet. These physical characteristics are considered cold-climate adaptations that prevent loss of body heat (Laughlin 1980). Aleuts and Eskimos have similar frequencies of blood group markers: ABO, MNS, and Rhesus systems, and other classic genetic markers (Laughlin 1980, Rychkov and Sheremetyeva 1972), and molecular genetic markers including mitochondrial DNA haplogroups A and D (Merriwether et al. 1995, Rubicz et al. 2003, Saillard et al. 2000). While the Aleuts exhibit high frequencies of haplogroup D, and lower A, the Eskimos have a high frequency of A and much lower D.

This thesis compares anthropometric measurements for the Pribilofs Islands Aleuts of St. Paul and St. George, with the St. Lawrence Island Eskimos of Gambell and Savoonga.

Figure 2. Diagram of Laughlin's theories about the origins of Aleuts and their American Eskimos and Amerindians (Laughlin and Harper 1979).



I. Linguistics: Aleut-Eskimo Language Family

Aleut and Eskimo languages belong to the same language family (Eskimo-Aleut), which, based on glottochronology (Greenberg et al 1985) estimates diverged between 5,000 and 11,000 years before present (yBP). Dumond (1977) suggests that Chukchi be added to this language family as a third branch as it is equally similar to both Aleut and Eskimo as each are to one another (Byard 1981, Dumond 1977). No close affinities have ever been clearly established between the Eskaleut language family and any other Native American language family lending support to the hypothesis that these ancestral populations are a result of an isolated recent migration from Siberia (Byard 1981).

The Aleut language is spoken throughout the Aleutian Island Chain and the Commander Islands by ~720 people (Ruhlen 1991). This language can be further subdivided into an Eastern and Western dialect, both equally intelligible, with a possible third Central dialect. It is possible that as many as seven dialects covered the island chain at one time (Rubicz 2001).

Eskimo language groups have a more complicated relationship when contrasted with Aleut. This is to be expected given the wide distribution of Eskimos from Siberia across Alaska, northern and eastern Canada and into Greenland (Ruhlen 1991). After the spilt between Aleut and Eskimo branches the Eskimo language group further diverged into Inupik (also referred to as Inupiaq, Inupiat and Inuit) and Yupik (Ruhlen 1991, Rubicz 2007 and Byard 1981). There is a distinct barrier between these two language groups at Norton Sound, Alaska; with Yupik running South to the

Aleutians and West to the Eastern coast of Siberia. Inupik then runs East across Canada over to Greenland (Ruhlen 1991). Estimates for the divergence between Yupik and Inupik range from 150-1400 yBP depending on which two languages are being contrasted (Byard 1981). Yupik can be further divided into Alaskan Yupik and Siberian Yupik (Byard 1981 and Ruhlen 1991). Despite its political association with Alaska, St. Lawrence Island Eskimos are Siberian Yupik speakers. This is not surprising since the coast of Siberia is only 40 miles from Gambell, while Alaska is located another 100 miles to the East. These two branches of Yupik speakers are not mutually intelligible, and are just as separated from one another as are the Alaskan Yupik from the Inupik. Inupik dialects have a smoother transition across Canada and Greenland and are therefore mutually intelligible (Byard 1981).

II. Prehistory and Archaeology of Bering Sea Region

The Paleo-arctic Tradition was the first defined cultural tradition present in the American arctic. The Paleo-arctic tradition was brought by the early Eskaleut hunters from Siberia and could be found in coastal north and southwest Alaska ~10,000 years before present (yBP). By 9000 yBP the Paleo-arctic tradition arrived in the Alaskan peninsula (Dumond 1977). See Table 1 for an outline of the archaeological chronology of the region.

Throughout prehistory, the Aleuts have a rather consistent material culture referred to as the Aleutian Tradition. The Early Anangula phase of the Aleutian tradition occurred between 9000 yBP - 7000 yBP. These sites have been found in the

Eastern Aleutians (Knecht and Davis 2001). The oldest site in the Aleutians, the Anangula Blade site, held similar technology to that of Mainland Alaska and Siberia. Both the Anangula and Hog Island sites of the Aleutians date to around 8400 yBP (Laughlin 1951, 1975, 1980, Rubicz 2001).

The Pacific coast of the Alaskan Peninsula followed the Ocean Bay tradition ~6000 yBP (Dumond 1977). While approximately 5500 yBP, the Aleutian Tradition enters into its Late Anangula phase in the east. These sites resemble the Ocean Bay Tradition of Kodiak and Pacific Region sites (Knecht and Davis 2001). Starting around 4500 yBP, the Ocean Bay tradition clearly separated into the Kodiak tradition and the Aleutian tradition (Dumond 1977). With the removal of Ocean Bay tradition influences on Aleutian Tradition, the island chain entered the Margaret Bay Phase (Knecht and Davis 2001).

The Arctic Small Tool Tradition (ASTt) horizon descended from the Paleo-arctic tradition and was spread throughout the Bering Sea, northern Alaska, and across Canada to Western Greenland, by ~4000 yBP, and then slowly south to the northern reaches of the Alaskan peninsula (Dumond 1977, Dumond 2001). This tool tradition is characterized by certain styles of burins, reworked blades or flakes used for generalized cutting or scraping created using burin spall detachment (Dumond 2001); small bifacial side and end blades; and microblades (Byard 1981). Dumond (2001) claims there is evidence for a "partial intrusion" of ASTt in the region during the Margaret Bay Phase, but would not classify these areas as being integral to the ASTt (Dumond 2001). Instead, these cultural items offer evidence for contact with

mainland Alaska and/or the Kodiak Islands (Knecht and Davis 2001, Rubicz 2001). Instead, ASTt can be thought of as the first truly Eskimo cultural tradition (Byard 1981, Dumond 1977).

From 3000-1000 yBP, the Aleutian Tradition enters into its Amaknak Phase (Knecht and Davis 2001). It is during this phase that the earliest site is found in the Western Aleutians (Rubicz 2001).

Around 2800 yBP, ASTt gave rise to the Dorset tradition in the eastern arctic, including Canada and Greenland (Dumond 1977). In the Western arctic, ASTt shifted to the Norton Tradition at ~2500 yBP. The Norton Tradition includes the southern Alaskan peninsula, far north Alaska, the Bering Strait and surrounding islands, and the Chukchi Peninsula (Dumond 1977).

Evidence for continual occupation begins in St. Lawrence Island dating back ~2300 yBP (Byard 1981). The oldest evidence for Old Bering Sea culture was found on St. Lawrence Island, primarily around present-day Gambell, and adjacent Punuk Islands (Dumond 1977, Byard 1981). Very close dates have also been found in Siberia on a nearby coastal site. The method of gravel tempering pottery is present in all later Eskimo traditions was also born in Old Bering Sea culture found on St. Lawrence Island (Dumond 1977).

Sometime between 1500 and 900 yBP, Old Bering Culture stage diverges into Punuk and Birnirk cultures, which Dumond (1977, 2001) refers to as the Punuk-Birnirk stage of the Thule Tradition. Punuk culture covers St. Lawrence Island and the Punuk Islands, along with the small portions of the southern and northern coasts

of the Chukchi Peninsula. Birnirk culture covers the remaining coasts of the Chukchi Sea (Dumond 1977). Archaeological records do not indicate isolation between Birnirk and Punuk populations; instead, there seems to be some exchange of culture. This continued exchange would explain the difference between the dates for divergence of language and culture in this region. (Dumond 1987, Byard 1981).

At this same time archaeological evidence suggests cultural and biological exchange between Aleuts and Eskimos increases (Holland 2001). On Akun Island there are skeletal remains of "neo-Aleuts" or those that settled recently or had evolved apart from the other Aleuts and possessed brachycephalic skulls rather than the long dolichocephalic skulls of paleo-Aleuts (Holland 2001). The most notable differences in material culture between the paleo- and neo-Aleuts can be found in their burial practices; with the paleo-Aleuts burying their dead as inhumations, while the neo-Aleuts practice mummification. All sites dating before 1000 yBP are considered paleo-Aleut (Coltrain et al 2006). Sites in the Eastern Aleutians dating after 1000 yBP represent both the paleo- and neo-Aleuts with continual occupation until Russian contact (Holland 2001, Coltrain et al 2006). Ancient DNA analyses have revealed statistically significant differences in mtDNA haplogroup frequencies (Coltrain et al 2006). However, stone tools reveal a pattern of trade or contact between the Neo-Aleuts and Paleo-Aleuts. Aleutian tool assemblage patterns were similar to those found on the Kodiak Islands by 1100 AD. Holland (2001) believes that learning how to shape new tools from new materials would require extensive contact or migration into the Aleutians. The Late Aleutian Phase (1000 – 200 yBP)

did not reach the Near Islands until just before Russian contact (Knecht and Davis 2001, Dumond 2001).

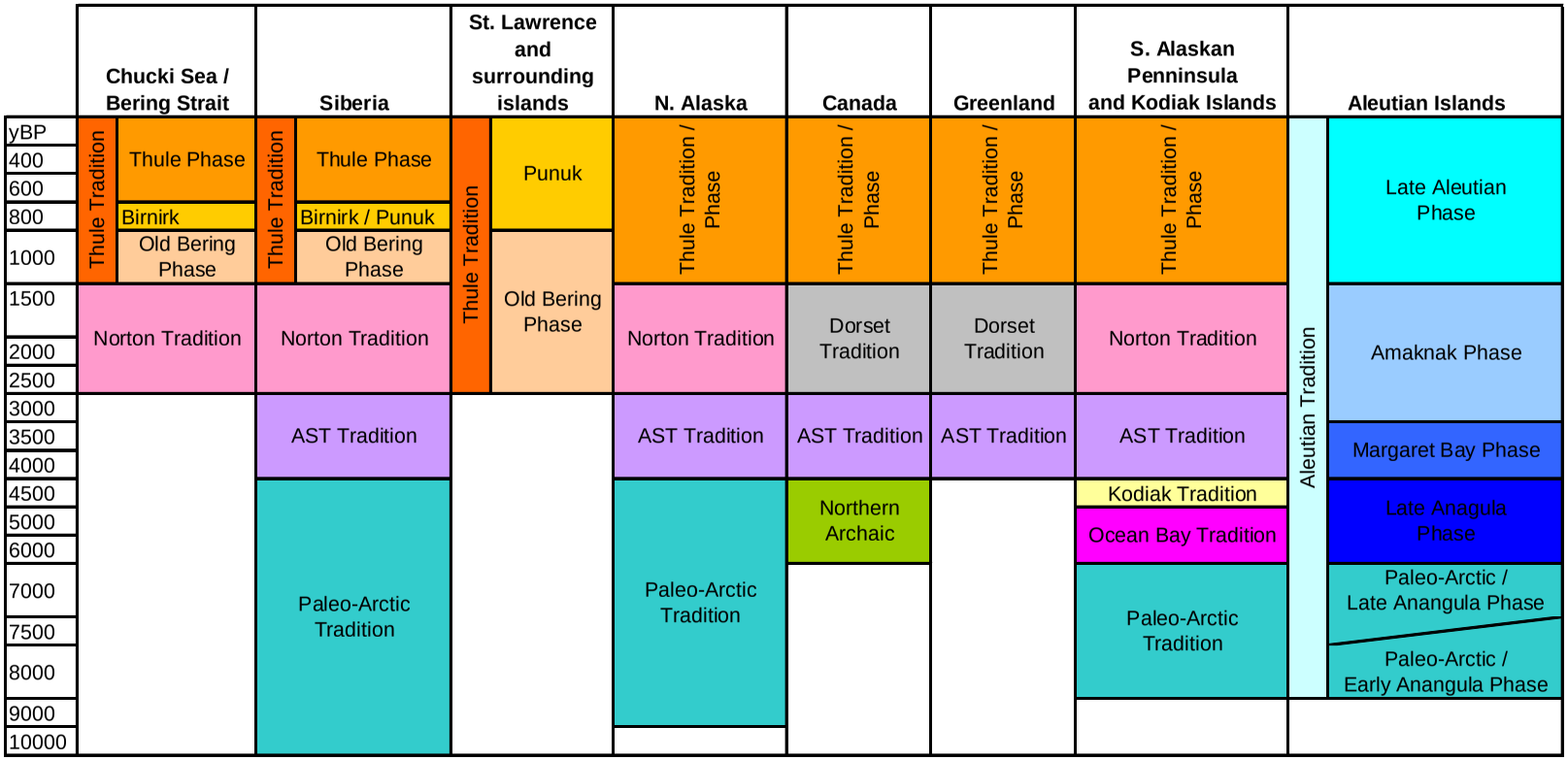
Approximately 1000-700 yBP, the Thule tradition spreads across Southwest Alaska, Kodiak Islands, then across Canada to Greenland overtaking the Dorset tradition (Collins 1937, Dumond 1977, Byard 1981). The advance of Thule culture coincides with the glottochronological estimates of the split between Inupik and Yupik languages (Collins 1937, Byard 1981). The current dispersion of the Inupik populations across Canada and Alaska seems contradictory to the rather smooth transition and mutually intelligible dialects within this language. However, archaeological evidence shows a back migration of the central Canadian Thule tradition, which pushed down into the Alaskan peninsula. This would also explain the sharp barrier between Yupik and Inupik languages in this region despite evidence that the Birnirk and Punuk populations had maintained contact (Collins 1937, Dumond 1977, Byard 1981). Along with cultural remains, skeletal remains also support a back migration from Central Canada. Therefore, linguistic, cultural, and biological evidence support the theory of a back migration of central Canadians into Alaska (Dumond 1977).

Radio carbon dates reveal that the Westward movement across the archipelago brought people to the Andreanof Islands by 5000 yBP, followed by the Rat Islands 3500 yBP, and finally the Near Islands 2500 yBP (Dumond 2001). “Prior to contact, the Aleut population was estimated to be 8,000-16,000,” (Derbeneva et al 2002: 416). Estimates of population sizes for St. Lawrence Island have been made either from

reanalysis of site reports or ecological models based on subsistence pattern and size of the island. At the time of European contact, the population size of St. Lawrence is estimated around 4000 people using site reports and 1500 people using an ecological model. Prior to European contact, there were an estimated 35 different villages and seasonal camps around the Island (Byard 1981).

In summary, phases of the Aleutian Tradition include the Early Anangula Phase (9000-7000 yBP), Late Anangula Phase (7000-4000 yBP), Margaret Bay Phase (4000-3000 yBP), Amaknak Phase (3000-1000 yBP), and the late Aleutian Phase (1000-200 yBP) (Knecht and Davis 2001). The presence of the earliest archaeological sites in the East and well above current sea level indicate that the path of settlement for the Islands chain came from the east rather from the west (Dumond 2001). Also, while it is apparent from the archaeological record that the Eskimo and Aleut cultural traditions diverged early after crossing the Bering Land Bridge, there is evidence of continued interaction and influence between these cultures. Contact between Eskimos and Aleuts seems to be primarily between the Yupik Eskimos rather than the Inupik Eskimos which spanned a much wider geographic distribution. As well, one can conclude from lithic, non-lithic, and skeletal remains that these populations come from a recent common ancestor, namely the Eskaleut hunters. Finally, both St. Lawrence Island and the eastern Aleutian Islands (Pribilofs parental population) remained relatively isolated from Inupik Eskimos as only minor influence of the Thule Phase of the Thule Tradition are present in the archaeological record.

Table 1. Chronology of Archaeological Occupation in the Bering Sea Region and Aleut-Eskimo Language Family (Dumond 1977, Collins 1937, Knecht and Davis 2001, Dumond 2001).



III. Biology

A. Morphology

There are a number of non-metric characteristics which distinguish the Aleuts and Eskimos from other Native Americans. Aleuts and Eskimos have a high frequency of the mandibular torus, a small protrusion on the lingual side of the mandible close to the canine. This protrusion appears in children, indicating its heritability, and is more frequent in men and in the eastern Aleutians. Native Americans tend to have a lower frequency of mandibular tori, but a higher frequency of palatine tori (Laughlin 1980, Laughlin 1951, Szathmary et al 1978). Aleuts and Eskimos also boast a low, broad ascending ramus (Laughlin 1980). They possess the "Mongoloid dental complex", which includes shoveling along the incisors, and the absence of the third molar (Laughlin 1980, Laughlin 1951, Szathmary et al 1978). Aleuts have a high frequency of three-rooted first rooted molar, especially in men (Laughlin 1980). Adding further support to an Eastern peopling, a cline in dental traits has been observed from East to West (Dumond 2001). Pre-Aleuts also possess a triangular occipital protrusion (Laughlin 1951). Based on a frequently cited study of discrete traits of the skull, St. Lawrence Island was more closely related to the Apache, a SW Athabaskan population, than Aleuts or other Eskimo populations; however, this study did not include the aforementioned traits that have been used to distinguish Eskimos and Aleuts from other Amerindians (Szathmary et al 1978).

Eastern origin for Aleuts is supported by the presence of paleo and neo-Aleuts in the east with the paleo-Aleut type spreading to the west (Laughlin 1951). The

paleo-Aleuts possess longer narrow skulls (dolichocephalic), while the Neo-Aleuts possess more rounded skulls (brachycephalic). These two types overlap in space and time in the Eastern Aleutians (Laughlin 1951, 1980). The distribution in cranial shape results in greater variation in head shape among eastern and western Aleuts than among combined Eskimo populations (Laughlin 1951). Far western Aleuts tend toward the dolichocephalic head shape of the Paleo-Aleuts, and cluster closer to Yupik Eskimos than other Aleuts, which cluster with Athapaskan Natives, when comparing frequencies of non-metric cranial features (Dumond 2001). There seems to be a reverse cline in the distribution of head breadth among the Eskimo, with greater round-headeness among western Eskimo (Laughlin 1951). While the western Eskimo have more rounded cranial vaults than do the eastern Eskimo, this characteristic is much more pronounced in eastern Neo-Aleuts. Both their broad skull and low cranial vault can be used to distinguish eastern Aleuts from their Eskimo neighbors (Laughlin 1980). Round headedness and short limb proportions are shared characteristics with Eskimo populations, but overall body size decreases in the Western Aleutians. (Laughlin 1951, 1980).

To better understand the relationships among Native Americans and Siberians, multivariate techniques have been employed to reanalyze data collected by Boas at the turn of the 20th century and Hrdlička from 1929-1931 (Ousley 1995). When using only Boas' data, Ousley's findings are similar to those of Szathmary and Ossenberg in that Aleuts do not cluster closely with Eskimo populations. Instead, Aleuts are most closely related to the Northwestern Amerindians, Kwakiutl and Bella Coola

(Ousley 1995). The Inupik Eskimo cluster with the Siberian Eskimo and the Chukchi and Koryak (Ousley 1995). However, Boas' data only represents Inupik Eskimos from North America and one sample of Siberian Yupik Eskimos (Ousley 1995). The relationship between Aleuts and Eskimos changes when Boas' data are combined with that of Hrdlička. The addition of several Southwest Alaskan and St. Lawrence Island Yupik Eskimos shows the close relationship between Aleuts and Eskimos (Ousley 1995).

The Fst values generated with Boas' anthropometric data are high when compared with other regions of the world, with combined Aleut and Northwest Coast Indians having an Fst of 0.27, and Siberian populations 0.12 (Ousley 1995). These estimates were generated assuming an h^2 of 0.42, which was determined using Boas' data on Southeastern Native Americans (Konigsberg and Ousley 1995). Therefore, these estimates assume equal heritability of anthropometric traits across all Native Americans and Siberians. These results are in concordance with previous genetic studies showing greater variation among Native American populations compared to Siberian (Torroni et al 1993).

Geography seems to play a larger role than linguistics in the relationships among Native Americans in the north (Jantz 1992, Ousley 1995). Not only do Aleuts cluster closely with their South Alaskan Yupik neighbors and St. Lawrence Island Eskimos, but they all cluster closely with the Kwakiutl and Bella Coola on the nearby Canadian coast. Also, Athabaskan speakers do not clearly cluster with other members of their own language phylum (See Figure 4, Ousley 1995). Using only Native

American populations from Boas's data, among-group variation in American Indian anthropometrics can primarily be attributed to differences in the head and face rather than post-cranial body measurements (Jantz et al 1992). One exception to the geographic patterning is found among the southwestern Athapaskans who recently migrated from the Subarctic. Instead of clustering with their neighbors in the United States, they group with the northwestern Athapaskans from Canada (Jantz et al 1992). Two of the canonical axes closely follow culture area and primarily show a separation of the Arctic (represented only by Inupik Eskimos) from other North American populations (Jantz et al 1992). Linguistic affiliation can explain only 38% of inter-population variation versus the 53% explained by cultural area (Jantz et al 1992). Those populations, considered linguistic isolates, appear to be morphometrically isolated as well. This seems to be most apparent among the Eskimo and the Wakashan (Jantz et al 1992). It is surprising that the St. Lawrence Island Yupik Eskimo cluster closely with Alaskan rather than Siberian Yupik Eskimos given their geographical and ethno-historical relationship with Siberian Yupik Eskimo, and considering previous studies have used this island as representative of Siberian Eskimo (Szathmary et al 1978) under these assumptions. This may be a result of recent admixture among the Siberian Eskimo and the Chukchi, or representative of the demographic effects of the back migration of Thule cultural phase which seems to have had a smaller influence over St. Lawrence Island than elsewhere (Ousley 1995, Byard 1981, Collins 1937).

The measurements with the greatest weight in among-population variation are nasal height, linear body measurements, head breadth and bizygomatic breadth (Jantz et al 1992). The separation of the Eskimo from other Native populations seems to be influenced by "small body dimensions, except shoulder breadth, with a high face and relatively narrow nose" (Jantz et al 1992: 450). Although, nasal height may be subject to greater interobserver error due to difficulty in locating the nasion (Jantz et al 1992).

The same rank is found when ranking geographic regions by stature and body mass (greatest to least: North American Indians, Eskimos, South American, Central American). Weight is more sensitive to geography than is height (Johnston and Schell 1979). There is no clear climatic explanation for the Central Americans to have shorter stature than the South American populations. We see a similar pattern in examination of the index of sitting height/stature in which Eskimo populations have a greater ratio as compared to South American Indians; as one would expect if Roberts's claims of adaptation of body size to environment are correct. However, several Central American populations (Nahua, Maya, Otomie) have even greater indices than the Eskimos (see Table 12.4 in Johnston and Schell 1979). Overall, Native Americans have greater weight/height ratios as compared to Europeans and Africans. This pattern develops early in the life cycle of Native Americans with greater average birth weights and becomes more pronounced as they enter childhood (Johnston and Schell 1979).

B. Genetics

i. Classical Genetic Markers

Previous analyses of red blood cell markers (RBCs) demonstrates that Eskimo populations tend to cluster with other Eskimo populations. Frequencies of ABO and MNS blood groups are so similar between the Eskimo and Aleut populations that Laughlin (1951) concludes they are one population. There is a low frequency of N for MNS locus, high A, and presence of B for ABO polymorphism in both Aleuts and Eskimos (Laughlin 1951).

Eskimos and Amerindians are equally related to Siberian populations using only RBCs and serum protein markers. Aleut and Eskimo frequencies are closer than either are to Athabaskans, but Koniag Eskimos show a closer relationship to Aleuts than do the other Eskimo populations do (Harper 1980). Using RBC antigen markers and protein markers the Paleo-Asiatic groups separate from the other Siberian groups due to their high frequency of the GM*AG haplotype and PGM1*1 allele. The Inupik Eskimos can be differentiated from the Chukchi and Yupik Eskimos by their high frequency of MN*M (Crawford et al 1997). Eskimo and Chukchi groups also exihibit much lower levels of heterozygosity when compared to other Siberian populations, likely due to the lower levels of gene flow. Most of this pattern can be explained by geography and the relative isolation of the Eskimo and Chukchi populations (Crawford et al 1997).

In a 1988 study of 31 classic genetic markers in Pribilof Aleuts and Kodiak Eskimos, Majumder et al (1988) found that the Aleut communities of St. Paul and St. George were genetically more homogeneous than the four Eskimo communities. This is to be expected considering Majumder et al excluded all individuals claiming any non-Aleut ancestry from the study. There were significant differences between the Aleuts and Eskimos for eight of sixteen polymorphic loci. In a dendrogram based on Nei's (1975) standard genetic distances among subpopulations, three of the Eskimo populations clustered together, while the fourth, Akhoik, was genetically closer to both Aleut communities than to the other Eskimos (Majumder et al 1988). Similarly, Crawford et al (1981) found western Aleutian populations cluster closely with Koniag Eskimos from Southern Alaska, which are also loosely clustered with the St. Lawrence Island populations. The relationship between Aleuts and Kodiak Islanders may be a function of to European gene flow into these populations (Crawford et al 1981), prehistoric contact between the populations (Holland 2001), or a combination of both scenarios. However, other studies have shown that classical markers cluster Aleuts with Siberian Eskimo, while the North American Eskimos form their own cluster (Szathmary et al 1978).

Furthermore, analysis of classic genetic markers (blood group and serum protein data) indicated there was considerable divergence between the villages of Savoonga and Gambell, likely due to founder effect compounded by intergenerational drift (Byard and Crawford 1991, Crawford et al 1981). Genetic drift appears to have had a greater effect on the population of Gambell, resulting in lower average genetic

heterozygosity (when considering only non-admixed individuals). Estimates of European admixture, based on gamma globulin markers, were slightly higher for Gambell than for Savoonga, but were small for both communities (8% and 4%, respectively) (Byard et al 1983). When compared with other populations, Savoonga was closer genetically to the Chaplino Eskimos of Northeastern Siberia, rather than to Gambell. This can be explained by a number of Savoonga males obtaining wives from the nearby Siberian community of Chaplino (Crawford et al 1981). The two Yupik-speaking St. Lawrence Island Eskimo communities clustered together when compared with the Inupik-speaking communities of Wales and King Island, Alaska, from which they were genetically distinct. Contrary to the findings of Ousley (1995), the St. Lawrence Island Eskimos show the greatest genetic affinity to the Siberian Eskimos, and as expected, based on language affiliation, geography, and ethnohistory of the circumarctic region, they cluster with the circumpolar group that includes Eskimos, Aleuts, and Chukchi, which differs genetically from other Native American and Siberian populations (Crawford et al 1981, Ferrell et al 1981).

Red blood cell and protein markers provide evidence for relative homogeneity among Inupik Eskimos when compared to Yupik Eskimos and Siberian populations, with St. Lawrence Island Eskimos intermediate between Inupik and Siberian populations. In contrast to the strong relationship between geography and anthropometrics, these studies reveal an association between language and genetics with only a secondary relationship to geography. All Inupik speaking Eskimos of North America, despite their widespread geographic distribution form a tight genetic

cluster. Yupik speaking Eskimos of St. Lawrence Island are intermediate between Siberian Yupik Eskimos and Inupik Eskimos. The relative heterogeneity of St. Lawrence Island can be attributed to the fission of Gambell when Savoonga was founded. As well, individuals from Gambell adopted admixed children from native groups in Alaska (Crawford 2007, Byard et al 1983). Of the two St. Lawrence populations, Savoonga is more genetically related to the Siberian populations of Chukotka. This is likely due to the gene flow between the two populations. Upon establishing the hunting village at Savoonga, the founding men took wives from nearby Chaplino Eskimos in Siberia, also closely related to Chukchi. In contrast, Gambell seems to have had greater European and Russian admixture (Crawford et al 1981).

GM allotypes are useful for differentiating populations due to large frequency differences and unique haplotypes existing within populations (Schanfield 1992). The most common Native American GM allotype is GM*AG, representing the majority of allotypes in all Native populations. The most common Asian allotype, GM*XG is not present among non-admixed Eskimos and appears only sporadically in other Native American populations. GM*AT is in appreciable frequency across all of North America and in Northern Asia. The southeast Asian haplotype, GM*AFB seems to be absent from Native Americans (Schanfield 1992). The founding populations of Eskimos in North American likely only possessed the GM*AG and GM*AT allotypes which differentiated them from the Nadene who also possess GM*XG with frequencies of all three allotypes similar to those found in Asia (Schanfield et al

1990). There is a clinal distribution of GM and KM allelic frequencies across North American Eskimo.

A maximum linkage cluster analysis using GM allotype frequencies reveals a three cluster pattern with all South Americans clustering together, all Central American and non-Nadene/Eskaleut North American Indians clustering together, and the third branch containing all Nadene, Eskaleut, and Siberian populations in the study with few exceptions. In the resultant dendrogram both Yupik and Inupik Eskimos occupy a single branch , then linked together with Canadian and US Plains Athapaskans, followed by the Chukchi (Schanfield 1992). In a similar study, the frequency of GM haplotypes clusters St. Lawrence Island Eskimos with other Yupik-speaking Siberian Eskimos rather than with Athabaskans or Inupik Eskimos (Byard et al 1983).

Using GM*FB as an indicator of European admixture, Gambell is estimated to have an 8% European contribution, while Savoonga has only 4.3%. Two nearby Inupik populations were also tested, with Wales having 7% admixture, and the GM*FB haplotype being absent on King Island (Byard et al 1983). Admixture estimates using geneaological information reveal only 5.6% for Gambell and 4.8% for Savoonga (Byard et al 1983). Admixture estimated in Southwestern Alaskan Eskimos is 2.1% (Peterson et al 1991).

One study revealed no relationship between estimates of admixture and heterozygosity. King Island, which seemed to have no occurrence of admixture has the highest average heterozygosity, while Savoonga, with intermediate estimates of

admixture, has the lowest average heterozygosity. Upon ranking the populations across loci, Gambell has the lowest rank for estimates of heterozygosity, but the highest estimate of European admixture (Byard et al 1983). These patterns make more sense when admixed individuals are separated from non-admixed natives. Admixed Eskimos do possess higher average heterozygosity while non-admixed participants of Gambell have the lowest average heterozygosity. The higher average heterozygosity of Savoonga despite its intermediate estimate of admixture is likely due to its larger populations size, the absence of the GM*FB haplotype among many of the known admixed individuals, and the prevalence for mating with Siberian rather than European women (Byard et al 1983). In addition, the small proportion of admixture is likely swamped by historical and pre-historical events that have led to bottlenecks and intergenerational genetic drift (Byard et al 1983).

Converting the distance ratios between these three populations and using the date of Anangula site of 9000 yBP as a calibration, estimates are possible for divergence times of these three linguistic groups. Given the spilt between Eskimo and Aleuts occurred 9000 yBP, the ancestral Eskaleuts diverged from the Athabaskans 14,985 yBP and the original founding populations for all considered dates to 18,918 yBP. The last divergence to occur was between the Yupik and Inupik Eskimo at approximately 5,162 yBP. The author uses the presence of ASTt across Alaska up until the Southern Alaskan Yupik region as evidence for support of the 5000 yBP divergence between Yupik and Inupik. However, current archaeological evidence shows ASTt influence even into the Koniag Eskimo range with some influence of

ASTt found among the Eastern Aleutians (Dumond 2001). The author argues that the equal distances among Athabaskans and Eskimos to Siberians is support for a single migratory wave of Athabaskan, Eskimo and Aleut ancestors (Harper 1980).

ii. Molecular Markers

a. Mitochondrial DNA

Probably the most studied genetic markers are those of mitochondrial DNA (mtDNA). These markers are useful for several reasons. It has been shown that mtDNA is almost entirely inherited through the mother and undergoes a constant mutation rate. This means that mtDNA is unlikely to undergo recombination, and therefore any changes in markers seen across generations can be assumed to be the result of new mutation. In addition, these mutations can be used to determine the separation of founding and offspring populations using the rate of mutation. Of further importance of mtDNA is that it rests inside the mitochondria of the cell, which are of great abundance; therefore, mtDNA is easier to obtain from degraded samples of tissue and archaeological remains than is nuclear DNA (Jobling et al 2004; Lalueza-Fox et al 2001).

There are five major mtDNA haplogroups that can characterize American mtDNA diversity: A, B, C, D, and X. Haplogroup A defined in America by a mutation at nucleotide position (np) 16111 involving a C to T transition and including HaeIII at np 633, has high frequencies in Alaska, Canada, the eastern US, and central Mexican Chibchan speakers. Haplogroup B is defined by the presence of the 9-bp

Region V deletion. Haplogroup B exhibits high frequencies in the Western and Midwestern US and is almost completely absent in arctic populations. Lineage C is defined by the loss of a *Hinc* II restriction site at np 13259. Haplogroup C is rare in most of NA, but in high frequency in South America. D is the loss of an *Alu* I restriction site at np 5176. Haplogroup D has higher frequencies in Alaska paired in consistently lower frequencies in the rest of NA, and in high frequency among South Americans along the Amazon (Torroni 1993a; Torroni 1993b; Bonatto and Salzano 1997; Crawford 1998; Lalueza-Fox et al 2001; Pereira et al 2005; Merriwether and Kaestle 1999; Merriwether et al 1995; Rubicz 2003; Salzano 2002; Schurr 2004; Sherry 2004). Involving a G to A mutation at np 16,213 and an addition of AccI at np14465, haplogroup X is found in high frequency in the Great Lakes and Greenland with moderately lower frequencies elsewhere (Rubicz et al 2003; Schurr et al 2004; Sherry 2004).

Haplogroup A is the most frequent mtDNA lineage among the Eskimos, Chukchi and Northern North Americans. Arctic and subarctic populations also possess high frequencies of D often to the exclusion of haplogroups B and C (See Table 2 for summary of frequencies in study populations). For the Aleuts, D is most prevalent and increases in frequency westward across the archipelago reaching fixation in the Commander Islands just West of the Aleutian Islands (Derbeneva et al 2002, Zlojutro 2006, Rubicz 2007, 2001, Rubicz et al 2003, Merriwether et al 1995). Higher frequencies of halpogroup A in eastern compared to western Aleutians may be

	A	B	C	D	Other
Gambell	0.58	0.00	0.14	0.26	0.02
Savoonga	0.939	0.00	0.00	0.02	0.041
St. Paul	0.407	0.00	0.00	0.593	0.00
St. George	0.172	0.00	0.00	0.828	0.00

Table 2. Summary of mtDNA haplogroup frequencies for study populations (Merriwether et. al. 1995, Rubicz 2007).

due to admixture with the southwestern Alaskan Eskimo populations (Rubicz 2007). Their high frequency of haplotype D conflicts with the increase of frequency A across North America from South to North (Zlojutro et al 2006). Some studies have found small frequencies of haplogroup C and "other" haplogroups among Eskimo populations in Siberia and the Americas and St. Paul Aleuts, but admixture cannot be ruled out as the cause of these (Hayes 2002, Merriwether et al 1995, Rubicz et al 2003, Rubicz 2007).

The greater resemblance between St. Paul and the Eastern Aleutian Islands is likely a result of St. Paul being largest of the historically founded populations thus making it less subject to genetic drift. Also, being on the US side of the Asian border, they have greater access to continued relationship with the parental populations in the East (Rubicz 2007). St. George has a much higher frequency of D and only two lineages of A, thus a lower level of gene diversity. Its smaller population size makes

it more subject to genetic drift (Rubicz 2007). Bering Island most resembles St. George due to its fixation of D. It too has a small population size, but is on the Russian side of the border limiting contact with the parental populations (Rubicz 2007).

Haplogroup frequencies on St. Lawrence Island are similar to those in other arctic populations. Both villages have high frequencies of haplogroup A, Gambell 58% and Savoonga 93.9%. The mtDNA haplogroup D is also present in appreciable frequencies in both Gambell (26%) and Savoonga (2%). Haplogroup C has only been documented on Gamebll (14%), while both populations have low frequencies of "other" haplotypes, Gambell 2% and Savoonga 4.1% (Merriweather et al 1995). The higher incidence of C and "other" haplogroups found in Merriwether et al (1995) is an indicator of differential gene flow into Gambell, probably due to a combination of native gene flow and adoption of children from the Alaskan mainland (Crawford 2007). It was also common for the Eskimos of St. Lawrence Island to select mates from the nearby Siberian community of Chaplino Eskimo (Starikovskaya et al 1998).

Ancient DNA (aDNA) analyses of Paleo-Aleut and Neo-Aleut have revealed similar frequencies of these halpogroups (28%-42% A and 58%-71% D) to those found in modern Aleuts of the eastern Aleutians and the historically founded population of St. Paul Island (D 59.3%-66.7%) (Hayes 2002, Derbeneva et al 2002, Rubicz 2007, Zlojutro et al 2006). Ancient Eskimo ancestors of the eastern arctic are also similar to modern arctic populations, possessing only A and D haplogroups. However, Dorset remains were fixed for haplogroup D, while Thule individuals

occupying the same region of Hudson Bay and Hudson Strait but temporally displaced were fixed for haplogroup A. This would seem to offer support for total replacement of Dorset population by the Thule culture (Hayes 2002).

There are conflicting results in modern haplotype frequencies in eastern Canada and Greenland (Saillard et al 2000, Helgason et al 2006). Saillard et al (2000) found a sample of 82 Inuit Eskimos from Western, Southern, and Eastern Greenland were fixed for haplogroup A (Saillard et al 2000). Conversely, Helgason et al (2006) did detect low frequencies of haplogroup D (4.3%) among his sample of 299 Greenland and Canadian Eskimo, primarily among Southern and Western samples. So, it is possible that this haplogroup was not detected earlier due to small sample sizes in these areas. There seems to be more variability with Greenland Eskimos than other circum-arctic populations. This geographic discontinuity can be explained by the advancement of Thule culture being an amalgamation of the Thule with the Dorset peoples rather than a total replacement (Helgason et al 2006).

Additionally, mtDNA can also shed light on the relationship between the Eskimo-Aleut language groups and their Siberian neighbors who share common ancestry. American natives have high levels of diversity across all populations compared to other continents and major regions, especially Siberia (Torroni et al 1993). Koryaks and Itel'men of the Kamchatka Peninsula in Siberia are maternally distinct from their geographic and linguistic neighbors, the Chukchi in Chukotka, as well as the Aleuts, Eskimos and Nadene Indians (Schurr et al 1999). Chukchi and Siberian Eskimo mtDNA haplotype frequencies are intermediate between Aleuts and

Inuit Eskimos (Helgason et al 2006). Three of the five founding haplotypes are represented among the Chukchi and Siberian Eskimo, A, C, and D, with A having the highest frequency in both (Starikovskaya et al 1998). Since haplogroup B is lacking in Eastern Siberia and the Pacific Rim Americans, it has been proposed that this is evidence for a separate migration for just haplogroup B (Torroni et al 1993). The presence of some Asian haplogroup G among the Chukchi is evidence for recent admixture with Kamchatkan populations (Starikovskaya et al 1998).

High resolution RFLP and HVS1 sequencing of mtDNA offers a more detailed picture of the relationships among Siberian, Arctic, Subarctic and northern North American Natives (Derbeneva et al 2002). The A2 founding haplotype, defined by 16111T mutation in the Hypervariable Sequence I (HVS1) region of the non-coding mtDNA molecule, A2 and its sub- haplotypes can be found throughout Chuckhi and Native American populations, and in the highest frequencies among Chukchi, Eskimos, and Nadene Indians (Saillard et al 2000, Zlojutro 2007). The high frequency (34%-51%) of the 16265G mutation within Eskimo and Chukchi A2 distinguishes these two populations from Nadene (Saillard et al 2000). This is an Eskimo-specific variant among Native Americans referred to as the A4 lineage. The Aleuts are easily distinguished by the presence of Aleut specific haplotypes A3 and A7 (see below for sequence determination), while the most common East Greenland haplotype A4 (66%) is absent from the Aleutians. (same as Helgason et al 2006 A2b) (Saillard et al 2000, Helgason et al 2006, Rubicz et al 2003, Rubicz 2007).

Aleuts possess only variants of haplotypes, A2 and D2, marked by the presence of 3316A, 16129A, and 16271C mutations. Of the Aleuts carrying A2, 91.1% possess a C-T transition at np 16192, also referred to as the A3 subhaplotype. In addition to the Aleuts, A3 and D2 can be found among Eskimo, Chukchi and Nadene Indians. Additionally, 12.1% of the Aleuts sampled possess an additional mutation at 16212A on A3, which denotes the Aleut specific A7 (Zlojutro et al 2006, Rubicz 2007). A median-joining network forms three star-like clusters surrounding these three haplotypes indicative of population expansions (Zlojutro et al 2006, Crawford 2007). Aleuts, like most North American populations have very little genetic diversity, representing the smallest estimates of gene diversity for D2 recorded so far (Zlojutro et al 2006). Intermatch mis-match distances for haplogroup A cluster Aleuts with Siberian and Greenland Eskimos, along with Chukchi and Athapaskans. Haplogroup D sequences clusters Aleuts with only the Siberian Eskimo and Chukchi while distinguishing them from other North American Native and Siberian populations (Zlojutro et al 2006, Rubicz 2007). Aleuts diverge considerably from the Koryak and Itel'men of the Kamchatka peninsula. Therefore, it is unlikely that there was any population movement from Kamchatka across the Aleutians, rather. There is also evidence for frequency distribution across the archipelago, which fits an isolation by distance model (Crawford 2007). These result support Laughlin's theory of peopling of the Aleutians from the east westward (Crawford 2007).

The entire Commander Island sample was fixed for the D2 haplotype (Derbeneva et al 2002, Rubicz 2007, Zlojutro et al 2006). An 8910A transversion was

described in several Aleuts from Commander which is absent from other Native American and Eskimos populations, referred to as Aleut specific D2b (Derbeneva et al 2002).

Several of the Aleutian samples group closely with the Siberian Eskimo, Chukchi and Athabaskans using mtDNA sequence data. Bering, St. George, Atka, and St. Paul form a closer cluster. Within this group, St. Paul has the closest relationship with the other Aleuts outside of the cluster (Crawford 2007). Sequence data shows significant differentiation between eastern, central, and western Aleutian Islanders; thus, providing support for the three dialect subdivision of the Aleut language (Crawford 2007).

Siberian and Alaskan Eskimos possess higher frequencies of D2 than do the Northwest Indians (Saillard et al 2000). There are four prevalent haplotypes and subhaplotypes among the Inuit. First is the A2 root (16111T), A3, A4, and D3 (16093C, 16173T, 16223T, 16319A, 16362C, 73G, 263G) (Helgason et al 2006). Eastern Greenland Eskimos are fixed for the A haplogroup, but do not show the A2 root type present among the other Eskimo, Chukchi and Nadene. Though, they do possess subtypes of A2 indicating that they are descendant from the same gene pool. This is not surprising considering that the A2 root type is rare among other Eskimo populations from Alaska and more common among the Nadene (Saillard et al 2000). Sequence divergence from Alaskan source DNA indicate that inhabitants of Eastern Canada and Greenland may be the result of interbreeding between the Thule and

Dorset cultures rather than a complete replacement of Dorset populations by Thule (Helgason et al 2006).

Koryak and Itel'men populations possess the founding A haplotype AM01 (A1) and founding haplogroups C and D in appreciable frequencies. However, high resolution sequencing does not reveal a close relationship between these populations and Native Americans. The absence of haplogroup B is not alarming as this haplogroup, while considered a founding haplogroup, is absent in all Siberian Eskimos, Chukchi and other Beringian and Arctic Native Americans (Schurr et al 1999).

Further evidence for a common ancestor of the Chukchi and Native Americans is the presence of haplogroup A 16111T mutation among all American Indians and the Chukchi, but absent from other Asian populations. The 16192T polymorphism separates Eskimos, Nadene and Chukchi from Amerindians. The presence of A4 separates the Chukchi and Eskimo from the rest of America (Starikovskaya et al 1998).

While the dates for the separation between Aleuts and Eskimos at ~9000 yBP is well accepted from the archaeological record, the population fission outside of the Aleutians is relatively unclear. Using the A2 founding type as a marker for the ancestral populations of all Eskaleut, Chukchi, Nadene, and Amerindian populations, we can date the emergence at ~24,800 – 29,964 yBP (+/- ~14,500) (Helgason et al 2006, Zlojutro 2006, Crawford 2007). Using the subhaplotype of A2 charcterized by 16192T, we see a separation of Arctic and Athapaskans from Amerindians around

6,300 +/- 3,900 yBP. The emergence of the Eskimo and Nadene specific 16265G mutation occurred 3,000 +/- 1,400 yBP (Saillard et al 2000). Using combined haplotypes A2, A3, A4, and D3, divergence estimates of Inuit populations from Siberian source gene pool range from 421 to 1147 yBP (Helgason et al 2006).

Using the Aleut specific subtype A7 and Aleut specific subtype D2b, we have coalescent estimates which overlap ~5000-6000 yBP. While these time estimates are not supported in the archaeological record, the estimate of the divergence times for Aleuts and Eskimos may be less than 9000 yBP due to continued admixture with the Koniag Eskimos, causing the Aleuts to delay becoming a genetically distinguished population immediately after settling in the Aleutians (Crawford 2007, Zlojutro 2006). D2 and A7 are signatures of a recent expansion of Aleuts, while A3 cluster is indicative of a more ancient expansion. The A3 expansion dates to 19,900, while the D2/A7 expansion dates to ~5400 yBP. This later date coincides with the Aleutian progression from the Eastern Islands to the West, while the A3 expansion may be a remnant of an early expansion of Beringian populations during the last glacial maximum (Zlojutro et al 2006, Rubicz 2007, Crawford 2007).

b. Y-chromosome Data

The Y-chromosome is useful for determining differential movements of males given that it is only passed down from father to son. The Y chromosome also carries extended regions in which there is no cross-over and large regions of repetitive seemingly evolutionarily neutral DNA. Contrary to the picture of mtDNA, Y-

chromosome estimates of diversity are rather high due to the high levels of non-native gene flow. In fact, a different Y haplogroup was observed for every male sampled on Bering Island. Of the Aleuts sampled, the lowest estimate of gene diversity was for St. George (Rubicz 2007). Ninety percent of the male lineages in St. Paul are non-native, while 89% of St. George and 87% of Aleutian Island males lineages are non-native (See Table 3 for frequency of Y-haplogroups in Pribilovians) (Rubicz 2007). The only Native American Y-chromosome haplogroup present among Aleuts is Q (Rubicz 2007). Based on Y haplogroup frequencies, St.George most resembles the Aleutian Aleuts with its high frequency of R, a European haplogroup, and low frequency of Q (Rubicz 2007). In addition to Q and R, St. Paul and Bering also exihibit N, I, and "other" haplogroups (Rubicz 2007). St. Paul and Bering are more closely related to one another and to Russian, Koryak, and Siberian and Greenlandic Eskimo due to the shared presence of non-native Y markers. Similarily, paternal lineages offer support for the close relationship between Chukotka and the Americas, as the DYS199 np 181T mutation is present throughout North American and the Chukchi (Starikovskaya et al 1998).

	Q	**R**	**I**	**J**	**N**	**Other**
St. Paul	0.10	0.30	0.15	0.05	0.2	0.2
St. George	0.1111	0.8889	0.00	0.00	0.00	0.00

Table 3. Frequency of Y-chromsome haplogroups based on SNPs for Aleuts of Pribilofs (Rubicz 2007).

c. Autosomal DNA

While genetic data cannot be used at this time to definitively discern the number of migrations into the New World, autosomal STR D9S1120 can show that all Native American populations share a recent common ancestor from Beringia rather than Asia. The smallest allele at this locus, 9 tetra-nucleotide repeats, can be found in appreciable frequencies in every population sampled from the Americas, along with the Chukchi and Koryak of Siberia. There are no recorded instances of a 10 repeat allele in the world. The high frequencies of the 9 repeat allele cannot be explained by selection or gene flow. Also, due to the lack of intermediately sized alleles, the most likely conclusion is that all Native Americans descended from a single source population located somewhere in Beringia. These findings are consistent with those of mtDNA and Y-chromosome (Schroeder et al 2007).

A close relationship among Siberian Yupik, Central Alaskan Yupik and East Greenland Inupik Eskimos is revealed by comparing frequencies of class II HLA alleles. All of these populations display high frequencies of DRB1*0401 and *1101, which are absent in other native populations (Leffell et al 2002). The Yupik Eskimos have relatively little variation at each locus within HLA as evidenced by each locus having a statistically significant negative deviation from Hardy-Weinberg Equilibrium due to reduced heterozygosity in the population. However, this reduction in heterozygosity is comparable to that seen at these loci across the Americas. This reduction is likely due to bottleneck effects from migration into the New World and devastation from diseases brought by Europeans (Leffell et al 2002).

In a separate study using HLA alleles by Moscoso et al (2007), Aleuts of Bering Island were genetically distinct from Eskimos, Chukchi, and other North American natives. Instead, Aleuts tend to cluster with Asian, Siberian, Russian, and Finnish populations. Eskimo population clustered together with Chukchi (Moscoso et al 2007). HLA frequencies indicate gene flow with Russians.

For Aleuts, estimates for heterozygosity in the Autosomal STRs are intermediate between diversity measures of mtDNA and Y haplogroups (Rubicz 2007).

IV. History

A. Aleuts of the Pribilofs Islands

Pre-contact estimates of population size for Aleuts range from 12,000 to 16,000, with ~10,000 in the Eastern Aleutians, 5,000 in the Central portion, and 1,000 in the Western portion. However, this population was reduced by 50% within 30 years after Russian contact, leaving only 1900 Aleut survivors in the Fox Islands by 1790 (Laughlin 1980). Much of the reduction in population was the result of mistreatment and slaughter of the Aleuts by the Russians followed by disease and famine that continued to decimate the populations after 1790. An increase in population size did not resume until after 1820 (Laughlin 1980).

At the time of Russian discovery in 1786, the Pribilof Islands were uninhabited (Lantis 1984). However, the Aleuts apparently knew of the existence of these islands, as legends tell of their accidental discovery by the son of an Unimak Island chief (Torrey 1983). As the summer residence and breeding grounds of the Northern fur seal, the Pribilof Islands were of great commercial interest to the Russians, particularly after the collapse of the sea otter population in the Aleutians due to over-hunting.

The Russians relocated Aleut hunters from Umnak and Unalaska Islands in the eastern Aleutians to the Pribilofs (Black 1983), where they were forced to harvest fur pelts. Fortunes were made by both the fur trading companies operating in the area, and the Russian treasury, until 1796 when the fur seal population was nearly decimated (Torrey 1983). The harvest continued indiscriminately until 1848, at which time protection was afforded to female seals in order to replenish the herds. In 1825, the village of St. Paul was established at its current location, and in 1830 the village of St. George was consolidated at its current location. In 1840, some St. Paul males were relocated to the Commander Islands to hunt sea otters (Derbeneva et al 2002).

In 1867, the US purchased Alaska from Russia, and with it came the Aleutian and Pribilof Islands and their inhabitants (Lantis 1984). The Pribilof Islands Aleuts officially became US citizens, although they were still required to hunt fur seals, first for the Alaska Commercial Company, and later for the US Department of Fisheries. By 1874 there were 222 Aleuts living on St. Paul, and 118 on St. George. Although

there have been population size fluctuations over time, St. Paul has always been the larger of the two populations.

At the start of WWII in 1942, the Japanese invaded the Aleutian Islands and captured the entire community of Attu and transported them to POW camps in Japan. As a result, all remaining Aleut communities in the Aleutians and Pribilofs were evacuated and placed in camps in Southeast Alaska. The Pribilof Aleuts, numbering 477, were taken to Funter Bay, located west of Juneau, and placed under the charge of the US Fish and Wildlife Department (Kolhoff 1995). The Office of Indian Affairs was responsible for all other relocated Aleut communities. Conditions in the camps were poor, but nonetheless, Aleuts were kept there for the duration of the war. In 1943, Pribilof Aleut men and school boys were permitted to return to St. Paul and St. George in order to do their part for the war effort by participating in the seal harvest. The US government stated that seal oil would not gel easily under cold conditions, and that fur seal coats would keep soldiers warm. By 1944, all Pribilovians had returned home, and by June of 1945, all Aleuts who wished to return were repatriated.

Upon their return, Pribilof Islands Aleuts struggled for independence, establishing their own village-level governments in the 1960s and gaining legal title to their land in the 1970s (Torrey 1983). By 1970, the Pribilof communities numbered 640 individuals, with 29 non-Aleut residents (see Table 4). Currently, there are an estimated 500 individuals living in the community of St. Paul, and 250 individuals living in St. George, with an increasing number of non-Aleuts entering the region,

due to easier access of the islands through commercial air travel and the promise of employment in the crabbing and fishing industries.

Place	Native	Other	Total
St. Paul	428	22	450
St. George	156	7	163

Table 4. Pribilof Island Aleuts in 1970 (Lantis 1984)

B. Eskimos of St. Lawrence Island

After Vitus Bering's first sighting of St. Lawrence Island in 1728, a number of other Russian and European explorers noted its presence and/or made contact with the island's inhabitants (Hughes 1984). The commercial whaling activities of the mid 1800's, in and around the North Pacific Ocean, and the Bering and Chukchi Seas, had a significant impact on the peoples of St. Lawrence Island. Although it is uncertain whether any shore stations were established by the whalers on St. Lawrence, it is clear that the inhabitants were involved in commerce with whaling vessels. Water, clothing, baleen, and ivory were exchanged for alcohol, firearms, and whaling equipment. Disease was also spread to local populations, often with devastating consequences.

Due to severe famine which struck 1878, the population of St. Lawrence Island was significantly reduced (Byard 1981, Hughes 1984). An estimated two-thirds

of the of the Island's inhabitants perished (see Table 5). Depletion of whales and walruses by commercial whaling vessels appears largely responsible for the depopulation, while other factors that may have played a role include: disease, alcoholism, reliance on trade goods (rather than storage of local foods), and unique climatic and hunting conditions. The survivors gathered at the village of Sivokak, which was later renamed Gambell, and they recruited additional migrants from mainland Siberia. In 1880, only 500 individuals remained at Gambell, and the St. Lawrence Island population continued to decline until it reached its nadir of 222 in 1917 (Byard 1981).

Table 5. Population size estimates for St. Lawrence Island (after Hughes 1984, and Byard 1981).

Year	**Prior to 1878**	**1880**	**1917**	**1950**	**1970**	**1980**
Population Size	1500	500	222	600	700	936

Recovery of the population was facilitated by the decline of commercial whaling which began in the 1880's (Byard 1981). In addition, reindeer were introduced to the island in 1900, and efforts were made to convert the hunters to herders. Younger individuals were chosen for this task, as they were more "progressive". They followed the herds to better pasture, eventually in 1917, establishing the village of Savoonga 40 miles to the east of Gambell. By 1920, there were 183 individuals living in Gambell and 95 in Savoonga. After recovering from

the famine that decimated St. Lawrence Island, many families adopted children from the Alaskan mainland. These children were often admixed natives (Byard et al 1983). Although only half the population size of Gambell, because of its youth Savoonga had nearly an equivalent breeding size, allowing it to eventually surpass Gambell in overall population size. By 1978, there were 402 individuals living in Gambell and 425 in Savoonga.

V. Summary

This chapter provides background on the archaeological, linguistic, and biological data linking the Aleuts to the Eskimos, and highlights their relationship to other American and Siberian natives.

Classical genetic and skeletal evidence support a close relationship between Eskimo and Athabaskan Indians (Szathmary et al 1978). Contrary to linguistic and genetic data, Aleutian skeletal populations often cluster closely with Northwest Coast or Plains Indians rather than Siberian or Eskimo populations (Szathmary and Ossenberg 1978, Ousley 1995). Conversely, cranial, morphological, dental, blood group, and molecular markers lump Aleuts together with Yupik Eskimo populations (Laughlin 1980, Jantz 1992, Ousley 1995). There is more concomitance among discrete traits with geography and linguistics than with measurable traits. Therefore, the traits included in the analysis will affect the outcome of the phylogenetic relationships (Ossenberg 1977). The most likely explanation is that there is a close genetic and morphological relationship between Eskimos, Aleuts, and Northwest

Coast Natives, but due to the great variation within the Athabaskans and between Inupik and Yupik Eskimos, the characteristics chosen for comparison will elucidate different relationships within this group.

It appears that different forces of evolution are operating on the genetic structure of the Aleuts, with genetic drift and founder effect having the greatest impact on mtDNA lineages and gene flow having the largest affect on paternal lineages (Rubicz 2007). Differential gene flow between the sexes is probably a result of Russian policies encouraging the marriage of Russian men to Aleut women (Rubicz 2007). The loss of male lineages is due in part to the violence of the Russians against the Aleut males, and the relocation of males to new hunting grounds (Rubicz 2007). Molecular, blood and morphological markers show a close association between Chukchi populations and North American Eskimos, Aleuts, and Indians versus southern Siberia populations in Kamchatka (Schurr et al 1999, Rubicz 2007).

The most likely time of entry for Native Americans was around 24,000 – 14,000 yBP when the Bering land bridge would have been exposed during the Wisconsin glaciation. Given that this is the most likely path taken, most of the archaeological evidence for this movement would now be under water (Harper 1980). This date of entry is supported by genetic data from Inuit and Aleut populations. D2/A7 expansion dates to ~5400 yBP (Zlojutro et al 2006, Rubicz 2007, Crawford 2007).

While it is apparent from the archaeological record that the Eskimo and Aleut cultural traditions diverged very early after crossing the Bering Land Bridge, both

archaeological and biological evidence supports continued interaction and influence between these cultures. Continued contact between Eskimos and Aleuts seems to be primarily between the Yupik Eskimos rather than the Inupik Eskimos which spanned a much wider geographic distribution and, according to genetic data, likely interbred with peoples of the Dorset cultures further differentiating them from the parental Alaskan gene pool. As well, one can conclude that these populations come from a recent common ancestor.

CHAPTER 3: MATERIALS

In 1979 William S. Laughlin measured Eskimo populations from St. Lawrence Island, followed by Aleuts from the Pribilof Islands in 1981. These anthropometric measurements were originally collected as part of a growth and development study of Bering Sea children (Johnston et al 1982). Original data sheets used by Laughlin were made available by the Museum of the Aleutians in Unalaska, Alaska. This analysis of the anthropometric measurements included Aleut participants from the Pribilofs: St. George (N= 165, 92 males and 73 females), and St. Paul (N=65, 32 males and 33 females); and Yupik-speaking Eskimo participants from St. Lawrence Island, Gambell (N= 61, 28 males and 32 females), and Savoonga (N=108, 51 males and 57 females). Only males and females over the age of 18 who were measured for all traits were included in this analysis. Laughlin's standard collection sheet included the following variables: stature, sitting height, biacromial breadth, elbow breadth, wrist breadth, knee breadth, upper arm circumference, total face height, upper face height, head length, head breadth, minimum frontal breadth, bizygomatic breadth, bigonial breadth, and triceps, iliac, and subscapular skinfolds. From these measurements indices were calculated for sitting height/stature, minimum frontal breadth/head breadth, minimum frontal breadth/bizygomatic breadth, bigonial breadth/bizygomatic breadth. In an effort to utilize the most heritable and informative measurements, all skinfolds and circumferential measurements were excluded from the analysis, leaving the following measurements: stature, sitting height, biacromial

breadth, elbow breadth, wrist breadth, total face height, upper face height, head length, head breadth, minimum frontal breadth, bizygomatic breadth, bigonial breadth, and the four indices mentioned above. Table 6 provides the mean values for all measurements used for each of these populations. For statistical analyses used for inter-population variation, individuals with missing data were excluded. However, total face height and upper face height could not be measured for some because of dentures. In these cases mean values were substituted for original data. All measurements were taken by Laughlin, thus, there is no inter-observer error.

Upon initial examination of Table 6, a few patterns emerge. Both males and females in St. George have the highest mean stature and sitting height of Aleuts and Eskimos, along with the greatest variation in each of these traits. Savoonga males have the shortest stature with the least variation, and Gambell females are the shortest of the females and Savoonga females have the least variation in stature. Sitting height shows the same pattern except Gambell males have the least variation. There seems to be no concordance across populations for breadth measurements of the body or skull. This is surprising considering St. Paul and St. George Aleuts are the result of relocation of Aleuts from the Eastern Aleutians, who are reported as having the broader skulls as compared to Eskimos. This pattern is not discernable in the means for bizygomatic, bigonial and head breadth. Among the populations, it would appear that Gambell would rank the lowest for level of within-group variation as it expresses the lowest levels of variation in males for elbow breadth and wrist breadth, which is

often used as a correlate for frame size. Overall, there seems to be few differences between means and variances for these traits across Aleuts and Eskimos.

Blood group and serum protein markers were compiled from the literature for comparison (Crawford et al 1981, Majumder et al 1988). A list of the markers and allele frequencies for the four populations are shown in Table 7. Some interesting differences between Aleuts and Eskimos arise from examining this table. For the ABO system, A2 is absent within Gambell and Savoonga, but present in the Pribiolfs (2-6%). Blood group B is higher in Gambell and Savoonga (12.5% and 9.4%) than in St. Paul and St. George (0.9% and 1.6%). For the Rh system, cde, considered a European marker, is approximately the same across Gambell, Savoonga and St. Paul (5.2% - 9%), but relatively high in St. George (16.1%). This is surprising considering that Majumder et al (1988) claims to have excluded all individuals with non-native ancestry. For the Duffy system, St. Lawrence Eskimos have higher frequencies of FY*A (88.7% - 100%) than do the Aleuts (62% - 78.2%), while the Aleuts have higher frequencies of FY*B than do the Eskimos. St. Paul has a higher frequency of Ms (60.5%) compared to the other populations (34.2% - 45.9%), while Gambell has the highest frequency of Ns (53% vs. 22.7% - 35.8%), and St. George has a relatively high frequency of NS (12.7% vs. 0.9% - 4.7%). For the Duffy system, Savoonga differs from the other populations in that it is entirely fixed for FY*A. For the remaining markers, frequencies are similar across populations.

Table 6. Means and standard deviation for Pribilofs Island Aleuts and St. Lawrence Island Eskimos.

Population	N	Stature (cm)	Sitting Height (cm)	Biacromial Breadth (cm)	Elbow Breadth (mm)	Wrist Breadth (mm)	Total Face Height (mm)
St. Paul (M)	92	165.91 +/- 7.10	89.13 +/- 3.35	40.15 +/- 2.50	74.47 +/- 5.03	60.27 +/- 3.66	123.67 +/- 6.08
St. Paul (F)	73	155.87 +/- 8.37	84.02 +/- 3.63	36.53 +/- 3.08	67.48 +/- 5.25	53.26 +/- 3.82	115.34 +/- 5.98
St. George (M)	32	170.28 +/- 8.61	90.72 +/- 4.8	40.85 +/- 3.15	74.25 +/- 4.03	61.44 +/- 3.13	125.88 +/- 7.37
St. George (F)	33	158.20 +/- 7.66	85.44 +/- 3.9	37.21 +/- 2.97	67.71 +/- 5.06	55.24 +/- 4.49	115.09 +/- 8.34
Gambell (M)	28	165.82 +/- 7.07	89.03 +/- 3.57	40.32 +/- 2.22	71.11 +/- 3.58	59.96 +/- 2.96	125.21 +/- 6.19
Gambell (F)	32	153.13 +/- 6.31	82.89 +/- 3.70	36.39 +/- 1.88	64.84 +/- 4.76	53.73 +/- 3.22	116.0 +/- 5.02
Savoonga (M)	51	163.89 +/- 6.27	87.98 +/- 3.97	40.19 +/- 2.20	71.56 +/- 3.98	60.74 +/- 3.07	124.69 +/- 6.34
Savoonga (F)	57	153.95 +/- 5.67	83.75 +/- 3.34	36.70 +/- 1.63	65.61 +/- 6.71	54.19 +/- 2.89	115.16 +/- 5.51

Population	N	Upper Face Height (mm)	Head Length (mm)	Head Breadth (mm)	Minimum Frontal (mm)	Bizygomatic Breadth (mm)	Bigonial Breadth (mm)
St. Paul (M)	92	70.87 +/- 4.2	195.44 +/- 6.42	157.48 +/- 5.48	109.16 +/- 6.11	146.47 +/- 6.85	111.5 +/- 6.68
St. Paul (F)	73	65.62 +/- 4.25	185.60 +/- 5.85	149.10 +/- 6.05	106.16 +/- 4.93	138.19 +/- 5.92	106.53 +/- 7.16
St. George (M)	32	72.82 +/- 5.44	196.22 +/- 6.31	158.75 +/- 5.54	108.41 +/- 5.25	148.28 +/- 5.03	110.84 +/- 4.33
St. George (F)	33	66.58 +/- 5.30	187.30 +/- 7.19	151.73 +/- 6.25	106.61 +/- 4.59	141.36 +/- 6.80	106.73 +/- 6.44
Gambell (M)	28	71.53 +/- 4.18	194.79 +/- 6.65	156.54 +/- 4.56	110.39 +/- 5.41	148.32 +/- 6.81	113.57 +/- 5.41
Gambell (F)	32	66.78 +/- 3.73	184.63 +/- 4.95	151.34 +/- 5.15	109.13 +/- 5.30	141.44 +/- 4.51	108.56 +/- 5.21
Savoonga (M)	51	73.24 +/- 5.95	193.49 +/- 6.65	157.82 +/- 6.40	108.80 +/- 5.15	149.47 +/- 6.06	113.86 +/- 6.65
Savoonga (F)	57	68.61 +/- 5.14	185.19 +/- 5.94	150.32 +/- 5.45	107.58 +/- 4.41	141.68 +/- 7.11	109.86 +/- 5.82

Table 7. Frequencies of Classic Markers for St. Paul, St. George, Gambell, and Savoonga (Crawford 1981, Majumder 1988).

		Gambell	*Savoonga*	*St. Paul*	*St. George*
ABO	*A1*	0.334	0.268	0.229	0.294
	A2	0.000	0.000	0.020	0.060
	B	0.125	0.094	0.009	0.016
	O	0.540	0.638	0.742	0.630
Rh	*CDE*	0.012	0.027	0.000	0.000
	CDe	0.533	0.476	0.540	0.581
	cDE	0.373	0.445	0.340	0.258
	cDe	0.000	0.000	0.027	0.000
	CdE	0.000	0.000	0.003	0.000
	Cde	0.000	0.000	0.000	0.000
	cdE	0.000	0.000	0.000	0.000
	cde	0.083	0.052	0.090	0.161
MNSs	*MS*	0.120	0.136	0.129	0.115
	Ms	0.342	0.459	0.605	0.434
	NS	0.009	0.047	0.040	0.127
	Ns	0.530	0.358	0.227	0.325

		Gambell	*Savoonga*	*St. Paul*	*St. George*
Kell	*K*	0.000	0.003	0.006	0.008
	k	1.000	0.997	0.994	0.992
Duffy	*FY*A*	0.887	1.000	0.620	0.782
	*FY*B*	0.113	0.000	0.380	0.218
Haptoglobins	*Hp1*	0.353	0.291	0.549	0.559
	Hp2	0.647	0.709	0.451	0.441
Adenylate kinase	*AK1*	0.994	1.000	0.997	0.992
	AK2	0.006	0.000	0.000	0.000
	AK6	0.000	0.000	0.003	0.008
6-PGD	*A*	0.994	0.994	0.984	1.000
	C	0.006	0.006	0.016	0.000

For comparative purposes, anthropometric measurements for North and Middle Americans were utilized (See Figure 3 and 4). North American natives were measured by Boas and a team of trained anthropometrists from 1890 to 1904 (Jantz 2006, Jantz 1995, Jantz et al 1992). Measurements of Middle Americans were collected across a large span of time, ranging from 1898 until 1952. No attempts were made in this study to correct for inter-observer error; however, Faulhaber discusses this issue in the original publication (Faulhaber 1970), and Jantz (1992, 2006)

addresses the same issues regarding Boas' data. Due to data collection being biased toward males (Jantz 2006) and possibly due to cultural biases regarding male measurements during time of collection, many populations within North and Central America have missing measurements for females, or the sample sizes for females are much lower than for males. In order to increase sample number and utilize as many measurements as possible for comparison, only males were used. Table 8 lists the populations used in this analysis and provides means for each measurement. The measurements were chosen to maximize the number of variables and sample size of the populations. As in previous data sets, the comparative data show the relative short stature and short sitting height of the Central and Southern Mexican natives to the other North American natives. Surprisingly, the Western Inupik Eskimo fit within the ranges for the Central and Southern Mexicans (stature 155.4-160.5 cm; sitting height 80.8-85.7 cm). Additionally, the Western Eskimo exhibit the smallest head breadth and head length for the Polar populations, but the largest bizygomatic breadth. The Crow are the tallest of all the Native Americans along with their neighbors, the Sioux, close behind. The most uniformity among geographical regions seems to be within the Central and Southern Mexican populations and the Polar samples exclusive of the Western Eskimo.

Figure 3. Map of locations for comparative populations in northern North America. Map created using Online Mapping Creation (Weinelt 1996).

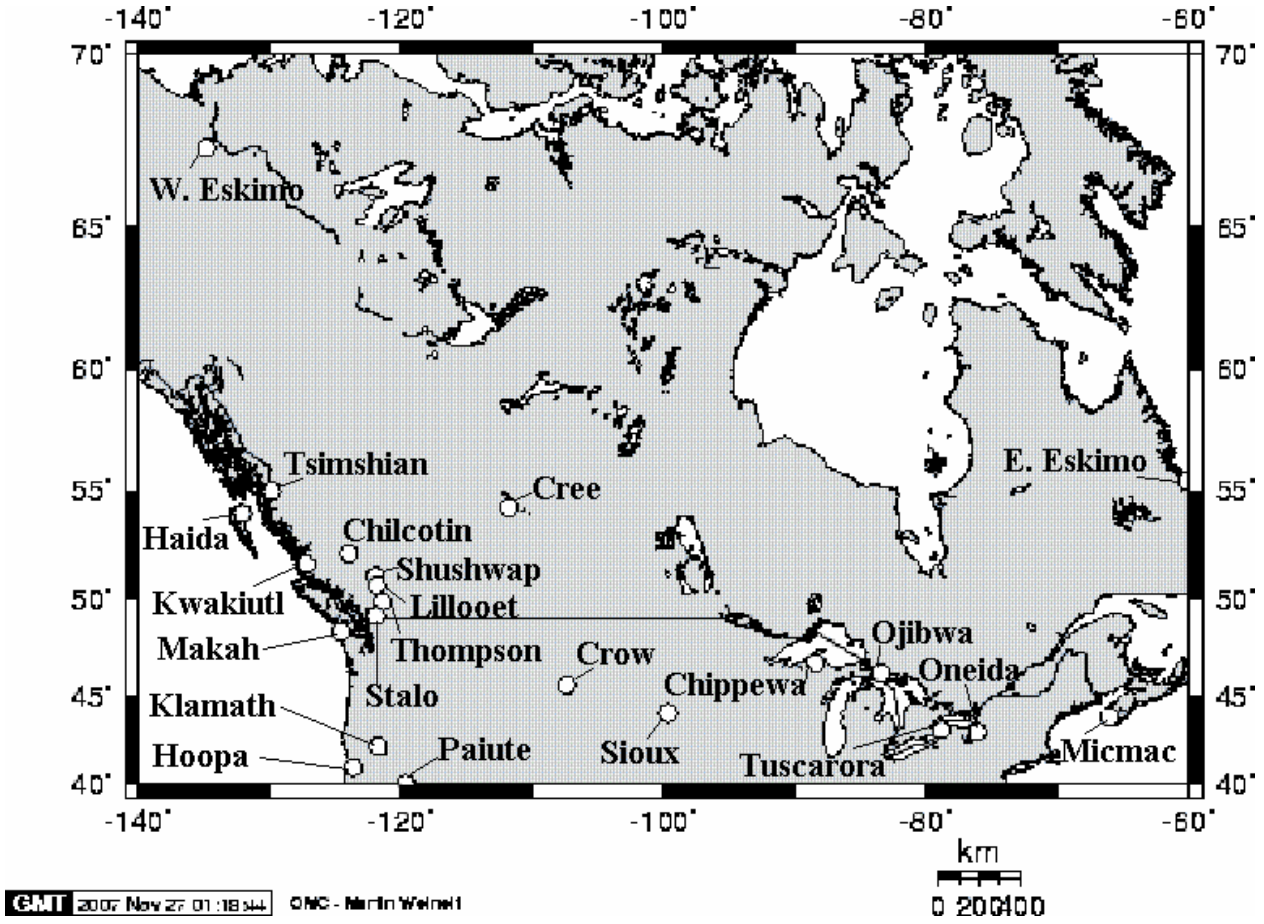


Figure 4. Map of locations for comparative data from Central U.S. to Southern Mexico. Map created using Online Mapping Creation (Weinelt 1996).

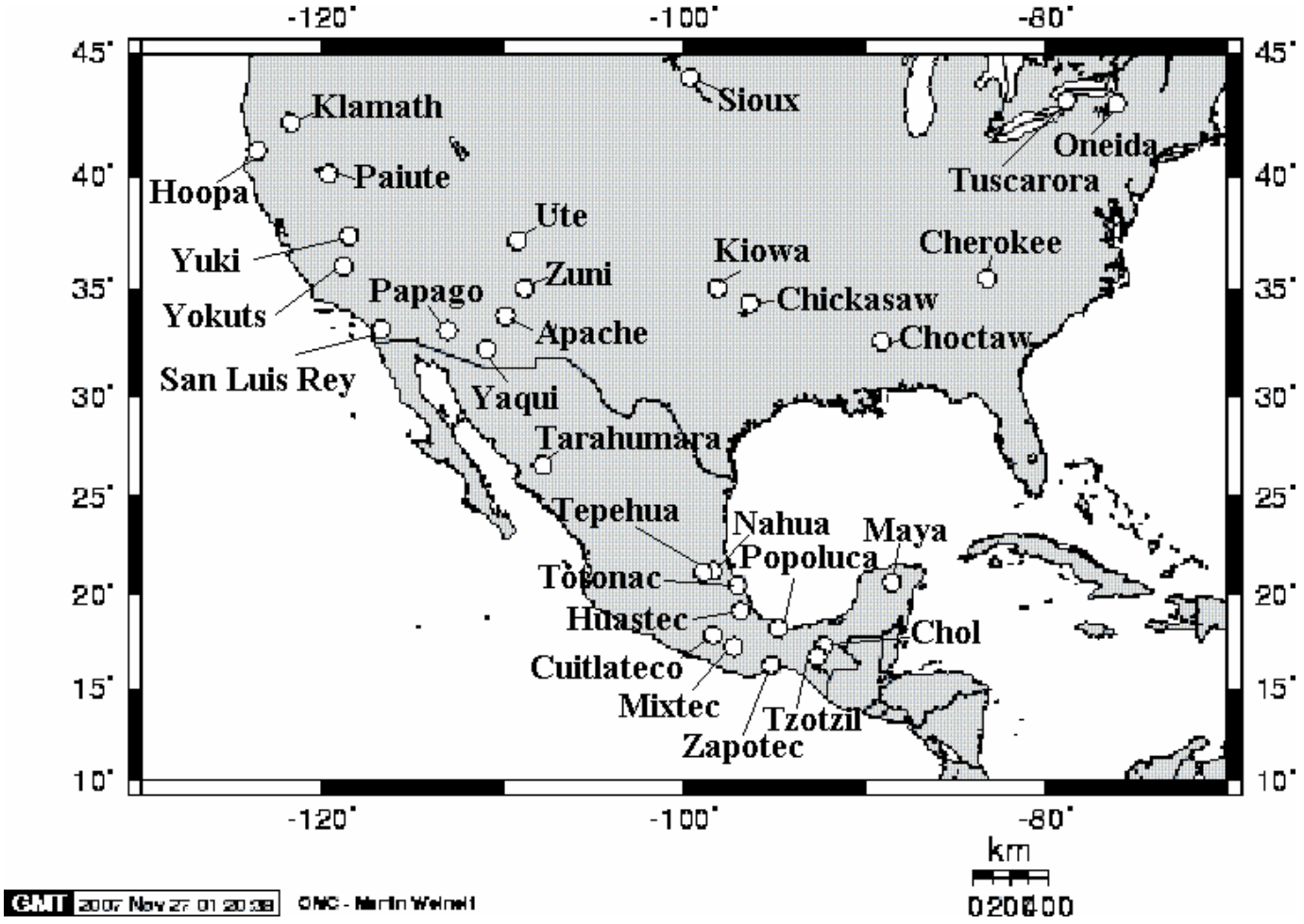


Table 8. Means for comparison between male Native Americans. Populations are numbered in descending order by latitude.

Code	Population	Region	Stature (cm)	Sitting Height (cm)	Head Length (mm)	Head Breadth (mm)	Bizygomatic (mm)
WEsk	**W.Eskimo**	Polar	167.852	88.236	191.840	149.040	151.240
Gam	**Gambell**	Polar	165.820	89.030	194.790	156.540	148.320
Sav	**Savoonga**	Polar	163.890	87.980	193.490	157.820	149.470
StP	**St.Paul**	Polar	165.910	89.130	195.430	157.480	146.470
StG	**St.George**	Polar	170.280	90.720	196.220	158.750	148.280
EEsk	**E.Eskimo**	Polar	156.735	83.135	192.154	152.115	145.115
TSI	**Tsimshian**	NW Coast	167.223	88.244	196.862	161.369	154.246
CRE	**Cree**	Subarctic	168.510	86.491	195.506	149.506	148.778
HAI	**Haida**	NW Coast	168.078	87.798	198.314	162.640	153.706
CHI	**Chilcotin**	Subarctic	164.594	86.352	185.647	158.294	146.029
KWK	**Kwakiutl**	NW Coast	163.330	88.841	193.869	157.887	150.419
SWP	**Shushwap**	Plateau	166.001	86.677	189.442	158.932	145.994
LIL	**Lillooet**	Plateau	160.972	84.323	185.589	160.167	148.867
TOM	**Thompson**	Plateau	161.912	84.614	188.816	156.326	147.149
STL	**Stalo**	NW Coast	163.203	86.368	188.898	165.746	152.661
MAK	**Makah**	NW Coast	164.367	87.909	187.826	160.457	156.348
CHW	**Chippewa**	Northeast	171.490	88.323	193.561	155.934	144.972
OJB	**Ojibwa**	Northeast	171.401	87.115	193.543	157.213	146.656
CRW	**Crow**	Plains	173.133	89.818	196.019	158.388	148.955
SIX	**Sioux**	Plains	172.321	88.473	194.374	154.946	148.151
MIC	**Micmac**	Northeast	172.740	88.625	191.546	150.682	143.647
TUS	**Tuscarora**	Northeast	171.213	88.990	192.966	153.600	143.367
ONE	**Oneida**	Northeast	171.873	89.973	194.463	154.731	146.224
KLA	**Klamath**	Plateau	167.884	87.944	182.097	159.344	143.602
HOP	**Hoopa**	California	166.518	85.544	180.178	152.318	134.556

Code	Population	Region	Stature (cm)	Sitting Height (cm)	Head Length (mm)	Head Breadth (mm)	Bizygomatic (mm)
PAI	**Paiute**	Great Basin	167.667	87.515	188.648	154.682	146.182
YUK	**Yuki**	California	161.250	84.058	194.690	149.793	146.655
UTE	**Ute**	Great Basin	165.321	86.306	191.417	152.472	146.528
YOK	**Yokuts**	California	170.257	86.195	192.000	162.095	150.190
CKE	**Cherokee**	Southeast	169.808	86.886	190.814	151.016	143.282
ZUN	**Zuni**	Southwest	161.770	85.918	181.676	150.915	143.014
KIW	**Kiowa**	Plains	157.830	82.142	182.027	147.676	138.108
CSW	**Chickasaw**	Southeast	168.934	87.896	186.927	148.853	141.706
SLR	**SanLuisRey**	California	169.915	85.841	185.753	161.507	149.479
APC	**Apache**	Southwest	169.294	88.455	181.788	161.127	149.424
PAP	**Papago**	Southwest	168.800	87.300	186.700	150.200	142.200
CTW	**Choctaw**	Southeast	170.921	84.487	186.318	151.109	144.582
YAQ	**Yaqui**	Southwest	166.700	83.100	183.800	149.200	141.000
TAR	**Tarahumara**	North Mexico	163.000	83.500	190.000	145.000	140.000
NAH	**Nahua**	Central Mexico	157.000	84.400	176.000	150.800	139.000
TEP	**Tepehua**	Central Mexico	157.700	85.700	179.800	153.900	143.900
MAY	**Maya**	Central Mexico	156.400	80.800	182.600	155.600	142.300
TOT	**Totonac**	Central Mexico	158.000	83.900	176.600	155.000	141.600
HUA	**Huastec**	Central Mexico	157.200	83.900	176.700	148.800	141.500
POP	**Popoluca**	Central Mexico	160.500	83.700	178.900	152.200	143.200
CUI	**Cuitlateco**	Central Mexico	161.100	85.200	174.900	150.500	138.700
CHL	**Chol**	Central Mexico	158.500	83.200	185.700	149.600	140.900
MIX	**Mixtec**	Southern Mexico	156.100	81.600	182.500	149.400	142.500
TZL	**Tzotzil**	Southern Mexico	158.400	84.700	184.200	144.200	130.500
ZAP	**Zapotec**	Southern Mexico	155.400	82.200	183.300	148.900	138.900

CHAPTER 4: ANALYTICAL METHODS

I. Variation Among Aleuts and Eskimos

The Relethford-Blangero method was employed to examine the phylogenetic relationship between Aleuts and Eskimos of the Bering Sea (Relethford and Blangero 1990). This method is based upon a method for examining interaction of gene flow and genetic drift based on the frequency of genetic markers developed by Harpending and Ward (1982). The Relethford-Blangero analysis compares the observed within-group variation with the expected within-group variation based on the distance of each population to the regional centroid (r_{ii}) and the average within-group variance for the populations, where

$$E[Vi] = \frac{Vw(1 - rii)}{1 - Fst} \qquad (1)$$

and V_i is the average phenotypic variance for the i^{th} population, and assuming that all traits have already been standardized; V_w is the average phenotypic variance across populations; and r_{ii} is the distance to the regional centroid (diagonals of the R-matrix).This is comparable to Harpending and Ward's (1982) estimate of expected heterozygosity, as shown

$$E[Hi] = Ht(1 - rii) \qquad (2)$$

H_i is the heterozygosity of the i^{th} population and H_t is the average heterozygosity across populations. The Relethford-Blangero method operates on the assumption that a linear relationship exists between average within group phenotypic variation and the distance to the regional centroid. Deviations from the models are shown as deviations from the expected within-group phenotypic variance. These estimates are used to create a distance matrix. The eigenvectors are then scaled and weighted using estimations of population size at the time of collection (Relethford 1996, Relethford et al 1994). A Principal Coordinates analysis was performed on both the scaled and unscaled R-matrices in order to provide a visual representation of the variation based on two axes. Matrices that have been scaled using population weights offer the benefit of observing relationships among populations exclusive of effects of stochastic processes (i.e. genetic drift), and thus highlighting population history (relationships based on gene flow or shared ancestry) (Relethford 1996). Therefore, any differences between scaled and unscaled R-matrices may be due to the opposing forces of genetic drift and population history acting upon populations.

A minimum F_{st} value is calculated in order to estimate the degree of population substructure found within the region (Relethford and Blangero 1990, Relethford et al 1997, Relethford and Harpending 1994, Williams-Blangero and Blangero 1989). Since phenotypic variance contains both components of genetic variance and environmental variance, $\sigma_P^2 = \sigma_G^2 + \sigma_E^2$, then one can assume that, $\sigma_P^2 \geq \sigma_G^2$ (Williams-Blangero and Blangero 1989). F_{st} can be estimated from r_{ii},

which is inversely related to σ_P^2, making all estimates of population divergence using phenotypic variance less than or equal to estimates made from an R-matrix of genetic variance. Genetic variance estimates can be obtained by scaling the minimum F_{st} by the heritability (h^2) of the trait under consideration, given that F_{st} and minimum F_{st} are related in the following manner (see equation 3) (Williams-Blangero and Blangero 1989, Relethford and Blangero 1990, Relethford 2007)

$$F_{st} = \frac{MinimumF_{st}}{MinimumF_{st} + h^2\left(1 - MinimumF_{st}\right)} \qquad (3)$$

Since the Relethford-Blangero method is attempting to ascertain the genetic relationship among populations from phenotypic traits, it is important to include heritability when comparing populations with significantly different genetic backgrounds. However, heritability of each measurement is unknown for the Aleuts of the Pribilofs and Eskimos of St. Lawrence. Given previous studies have found that Alaskan Eskimos and Aleuts are closely related (Ousley 1995, Jantz et al 1992), it is reasonable to assume that the heritability of these traits is similar. Since, the heritability is given as 1, this measure provides a minimum F_{st}. Additionally, previous studies have shown no significant changes in the overall relationship among populations when altering the h^2 (Relethford and Blangero 1990, Roseman 2004). For exploratory purposes a heritability was used in one instance to examine any possible alterations. Heritability of 0.42 was determined using Cherokee, Chippewa, MicMac,

Mississauga, and Ojibwa and using 12 traits (leg length, arm length, shoulder height, figer reach, sitting height, shoulder breadth, head length, head breadth, face height, bizygomatic breadth, nose height, nose breadth) all using Boas' original data (Konigsberg and Ousley 1995). Keep in mind that this heritability estimate may not accurately reflect the heritability of traits in the Aleut and Eskimo communities under study due to extreme environmental history of these populations (Johnston and Schell 1979: 276).

All analytical methods described above were performed using the computer program, RMET version 5.0 (Relethford 2003). Before data were entered, each measurement was regressed against age, and the resultant residuals were used to eliminate any affects of age on the variables. To remove any effects of gender, these residuals were then standardized using z scores before pooling males with females. To assess phylogenetic relationships through plots, Principle Coordinates of R-matrices were entered into NTSYSpc version 2.02h (Rohlf 1998).

Nei's genetic distance matrix (1972) was constructed using the allelic frequencies from the classical genetic markers. The genetic distances were then compared to the distance matrix (d-hat) of anthropometric measurements using a Mantel randomization test using NTSYSpc version 2.02h (Rohlf 1998).

II. Variation Among North American Natives

To understand the relationship connecting Aleuts and Eskimos to other Native Americans several additional tests were performed using the materials described above. Anthropometric distance and geographic distance matrices were constructed. A Euclidean distance matrix was constructed using the means for each measurement for the males within each population mentioned. Euclidean distance was calculated using NTSYSpc version 2.02h (Rohlf 1998). The geographic distance matrix was calculated using GEOG 2.1 (Relethford 2000). This application utilizes longitude and latitude to calculate great circle distance. In most cases, the longitude and latitude was easily obtained by looking up the location for the collection city. However, in cases in which there was more than one collection location, longitude and latitude were estimated using a city central to all localities from which samples in the population were taken. In cases where longitude and latitude for one city was unavailable (as in cases where cities have changed name since time of collection), longitude and latitude were taken from a location centered among the remaining localities.

In order to examine the relationship of phenotypic variation and geography, a Mantel randomization test was run between the Anthropometric distance matrix and the geographic distance matrix. A Mantel test involves holding one matrix constant and creating a randomly configured matrix from the second, then creating a correlation statistic for the constant matrix and the randomized matrix. A distribution of the correlation statistics is created from the randomization tests performed. The correlation between the two original distance matrices is then compared to the

randomized correlation distribution to see if the results are significant. If there is no true relationship of the two matrices, then one would expect that the correlation between the two distance matrices would be similar to the correlation among any of the randomly created matrices and the constant matrix. However, if there is an underlying relationship, then one would find that the correlation is somewhat higher or lower (depending on a negative or positive correlation) than the average random correlation. Mantel tests were performed using NTSYSpc version 2.02h (Rohlf 1998). This test was run with 3000 randomization attempts. Since there are 50! possible random matrices that can be generated from the original distance matrices, the numbers were decreased to lower the computation time and fit within the limits of the computer program. Since previous studies on North American Indians have not found a strong relationship between geography and phenotypic distance, but rather a relationship with distance in longitude (Jantz 2006), a Mantel test was then performed using only North Americans, and a separate one on Meso-Americans. A distance matrix based on latitude and one on longitude were also generated and then compared to Anthropometric distance. Only a negligible increase in correlation was seen when permutations were increased past 3000.

A Neighbor Joining Tree (NJT) was constructed using the Anthropometric distance matrix. The purpose of a NJT is to create a topology that minimizes the total branch length for the tree, or in other words, represents the tree with the shortest evolutionary time based on the given distance matrix. The purpose of NJT is to visualize the relationship between these populations, but by examining at the most

likely closest “neighbor”, or closest operational taxonomic unit (OTU) (Saitou and Nei 1987). This can supply a means to infer not just overall relatedness, but possible phylogenetic relationship. As with any transformation of data, some information is lost when the Anthropometric distance matrix is transformed into the NJT. To assess the fit of the tree to the original data, a cophenetic distance matrix is created from the tree and then compared to the original Anthropometric distance matrix using a Mantel randomization test. The NJT, cophenetic matrix, and Mantel randomization test were performed using NTSYSpc version 2.02h (Rohlf 1998).

Principal Components Analysis (PCA) was performed on the population means using a correlation matrix to provide another method for describing the variation among populations on fewer axes, as well as provide information on the weight of the variables in separating the populations. PCA attempts to compress the data into few axes for a visual representation of the relationship among populations. PCA achieves this by running an eigenanalysis on the original matrix, then plotting the scores of the objects on the specified number of axes. So, PCA is using the variation among the variables (in the case of an eigenanalysis of a variance-covariance matrix) or the correlations among the variables among the populations to create the “components”. PCA was performed using NTSYSpc version 2.02h (Rohlf 1998).

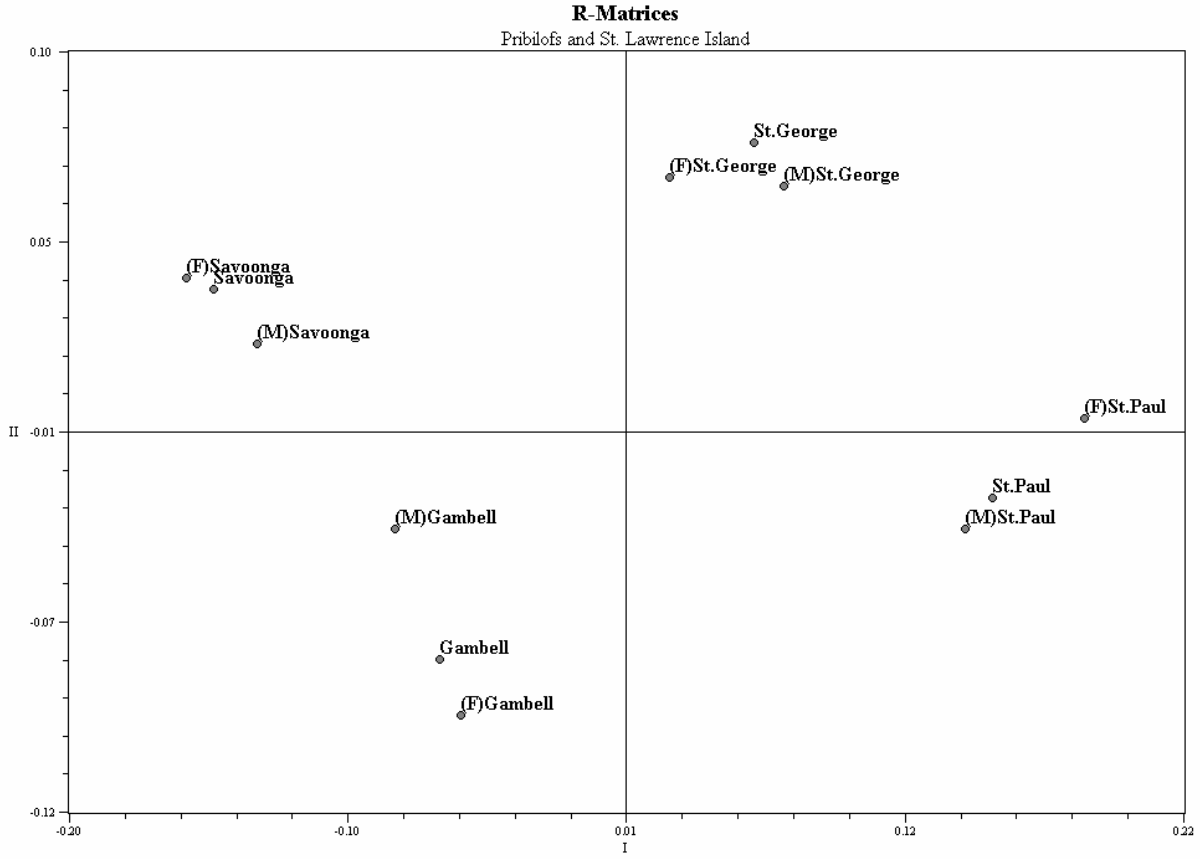
CHAPTER 5: RESULTS

I. Bering Sea Natives

When only females from the four Bering Sea populations were examined using the twelve original measurements, resulting in a Minimum F_{st} value of 0.027383 and an Unbiased Minimum F_{st} = 0.016537. This would indicate, as expected, that there is little population substructure among the females in this region. Both Eskimo populations of St. Lawrence Island have less than average phenotypic variance (Appendix B). For the R-matrix analysis, 97.9% of the variation is accounted for on the first two axes with 79.9% and 18.0% respectively. In Figure 5 the first axis is separating the Aleuts from the Eskimos, while the second axis clusters St. Paul with Gambell and St. George with Savoonga. St. George is the closest population to the centroid.

For the males, a Minimum F_{st} of 0.02059 and unbiased Minimum F_{st} of 0.0106 were obtained. Again, this indicates that there is very little phenotypic differentiation among the Bering Sea Natives (Appendix A). Overall, males seem to have a higher mean within-group phenotypic variance (0.939) when compared to the females (0.928) (Appendix B). This seems to be mostly due to the high within- group phenotypic variance of males from St. George. Similar to the findings in females, both Aleut populations deviate positively from expected phenotypic variance, while

Figure 5. Plot of first two principal coordinates from an R-matrix analysis performed using original 12 variables on males, females and whole population. Three plots are overlaid.



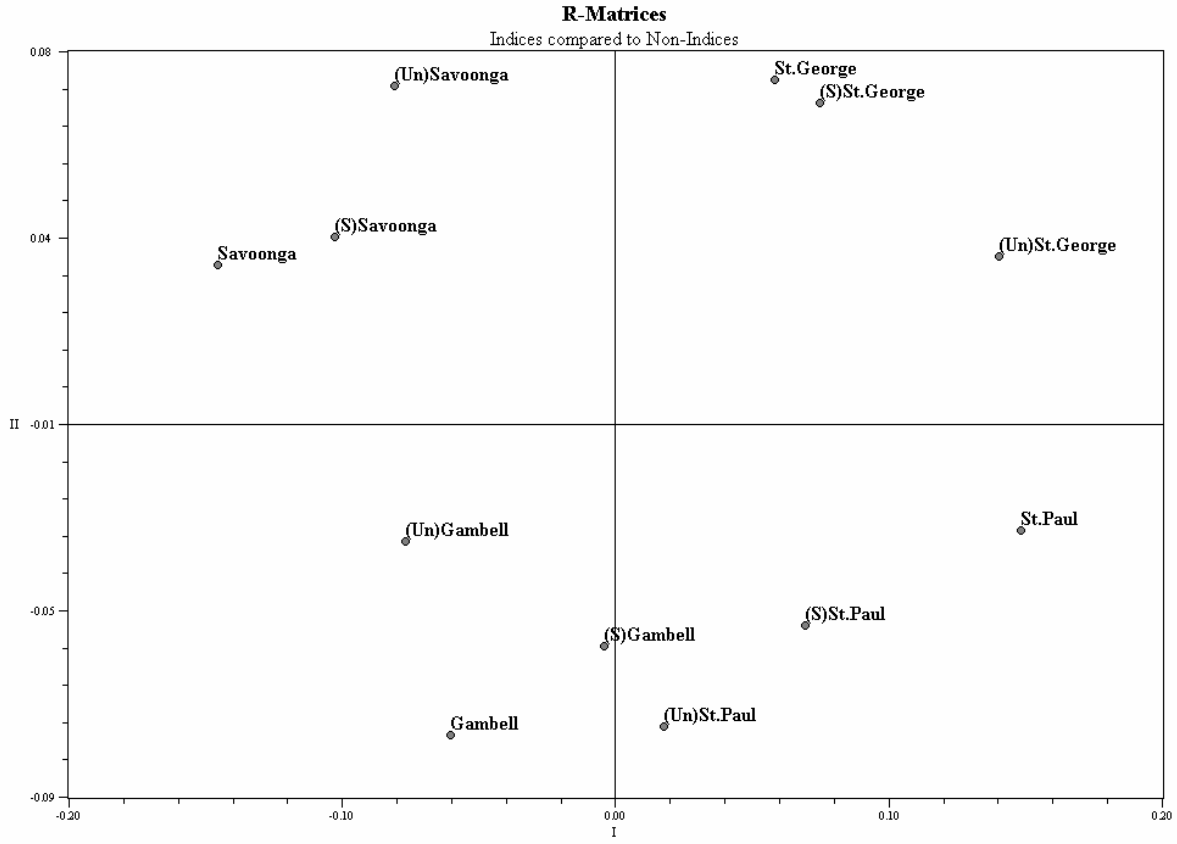
Gambell and Savoonga deviate negatively. The R- Matrix in Figure 5 accounts for 100% of the variation on the first two axes, with 87% on the first and 13% on the second. Gambell and Savoonga males cluster more closely than do the females for same or the Aleut males. Again, the first axis separates Aleuts from Eskimos, while the second axis clusters Gambell with St. Paul males. Gambell males are even closer to the centroid than are the females of Gambell.

In accordance with each separate gender, small values for Minimum F_{st} were again found when the sexes were pooled, with an Minimum F_{st} of 0.020527 and unbiased Minimum F_{st} of 0.014989. Similar to the results obtained from males and females, both Aleut populations deviate positively, while Gambell and Savoonga deviate negatively from expected within-group variance (Table 9). Within the Aleuts, St. George shows evidence of higher within group variance and higher r_{ii}, similar to the findings when examining males separately. Greater r_{ii} would be indicative of genetic drift operating on males of St. George, while greater phenotypic variation indicates greater gene flow. The R-matrix, shown in Figure 5, accounts for 97.3% of the variation within the data, with 77.3% on the first axis and 20.0% on the second. The picture is almost identical to that of the males, with the first axis clustering Savoonga with Gambell and St. Paul with St. George; and the second axis clustering St. Paul with Gambell and Savoonga with St. George. Savoonga is again furthest from St. Paul on the first axis. Unlike the results for females, Gambell is closest to the centroid, while St. George has the greatest r_{ii}.

For exploratory purposes, the Relethford-Blangero method was again applied using three subsets of the data. First an analysis was run dropping wrist breadth and elbow breadth, leaving the remaining ten original variables. All interpretations of variance are the same. The R-matrix analysis (not shown) was almost identical to that produced from the previously discussed plot created from all twelve variables. With only the four indices used for the analyses, the picture does change slightly. The Minimum F_{st} value based on these four variables is 0.0124 and an unbiased Minimum F_{st} of 0.0072 indicating there is even less variance among the populations in these body proportions. St. Paul is the only population to deviate positively from expected phenotypic variance, while St. George, Gambell and Savoonga exhibit less phenotypic variation than expected. The R-matrix illustrates the same relationship seen when considering the original twelve variables with the first axis separating Aleuts from Eskimos and Gambell and St. Paul clustering together along the second axis. However, the distance among populations is slightly reduced with the exception of St. George (See Figure 6). This model also exhibits the most noticeable difference between the scaled and unscaled R-matrices, indicating the affect of genetic drift on differentiating St. George from the other focus populations.

Finally, a model was used which included Ousley (1995) estimate of heritability ($h^2 = 0.42$) using Boas' data. This test resulted in an F_{st} of 0.0475 and an unbiased F_{st} of 0.0420. This estimate is far lower than any estimate of F_{st} using Boas' data (This study = 0.0420, Siberia = 0.12, Aleut and NW Coast = 0.27, NW Coast only = 0.26) (See table 7, Ousley 1995). This is indicative of the strong phylogenetic

Figure 6. R-Matrix plot comparing Aleut and Eskimo anthropometrics for original 12 variables with unscaled plot of 4 indices (Un) and scaled plot of 4 indices (S).



Males and Females Combined **Within-group Phenotypic Variance**				
Mean = 0.931				
Population	r(ii)	Observed	Expected	Residual
St. Paul	0.0228	1.014	0.927	0.087
St. George	0.0340	1.104	0.921	0.184
Gambell	0.0040	0.803	0.942	-0.139
Savoonga	0.0165	0.907	0.930	-0.023

Table 9. Estimates of within-group phenotypic variance, distance from the average centroid and deviations from expectation of phenotypic variance using the Relethford-Blangero method for twelve measurements on females and males.

relationship between Aleuts and Yupik Eskimos resulting in little phenotypic variation. However, as mentioned earlier, heritability may be higher in populations living in extreme environments, in which case, the estimates of F_{st} may decrease (See pages 61-63 for further discussion).

The Mantel test between the classic genetic markers and the Euclidean distance matrix created from the anthropometric measurements yielded a strong correlation (r= 0.69526), but not a significant one (p= 0.1643) (See Figure 7). It is not surprising that this correlation was not significant considering there are only 6 points of comparison. Comparisons between St. Paul with St. George and Gambell deviate from the expected correlation. This may be related to the data sets used for

comparison. In Majumder et al (1988) all individuals claiming non-Aleut ancestry were sampled but excluded from analysis; Crawford et al (1981) did not sample individuals that were non-Eskimo from St. Lawrence Island. In reviewing the blood markers, it is possible that some individuals of non-Aleut descent made it into the sample as indicated by the high frequency of RH cde in St. George and the many differences between St. Paul and the other Alaskan groups (see Table 7).

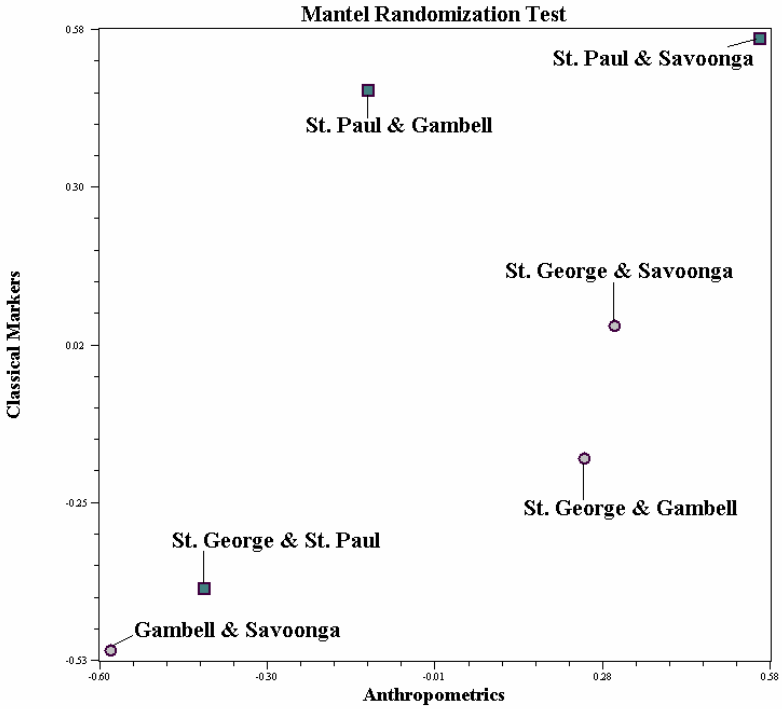


Figure 7. Plot for Mantel randomization test for correlation of anthropometric distance to distance based on classical genetic markers. Squares represent points comparing St. Paul to other populations.

II. Bering Sea Natives and Other North American Natives

The Euclidean distance matrix of anthropometric measurements was compared to a geographic distance matrix using a Mantel randomization test. A statistically significant correlation of 0.38392 was found between the two distance measures, with a one-tailed p-value of 0.0007. While there is a statistically significant relationship between geography and physique, it is not a strong one. The Mantel test comparing anthropometric distance to latitude revealed a correlation of 0.53240 with a p-value of 0.0007 (one-tailed test). Anthropometric distance and longitude revealed a small, only marginally significant (p= 0.033) correlation (r= 0.11519), making any interpretation of correlation difficult. Given that this is contradictory to previous studies, which have found patterns of stature and sitting height to follow an east to west pattern among North American Natives (Jantz 2006), the MesoAmerican populations were separated and distance matrices and Mantel tests were performed again. No significant correlation was found between anthropometric distance and distance based on circumference or longitude among North Americans, but a small marginally significant (p= 0.0427) correlation (r= 0.1403) was found between latitude and morphology. The highest correlation for northern North America was between anthropometric distance and circumferential distance with r= 0.1612 and p= 0.065. When Mesoamericans were considered by themselves all associations were significantly correlated. Aleuts, Eskimos and Mesoamericans exhibited a correlation of 0.804 between anthropometric distance and geographic distance with a p-value of

0.001. When highlighting individual points within the Mantel plots, one can see that the relationships among MesoAmericans and between the North American populations have the greatest influence on the overall relationship between geography and physique.

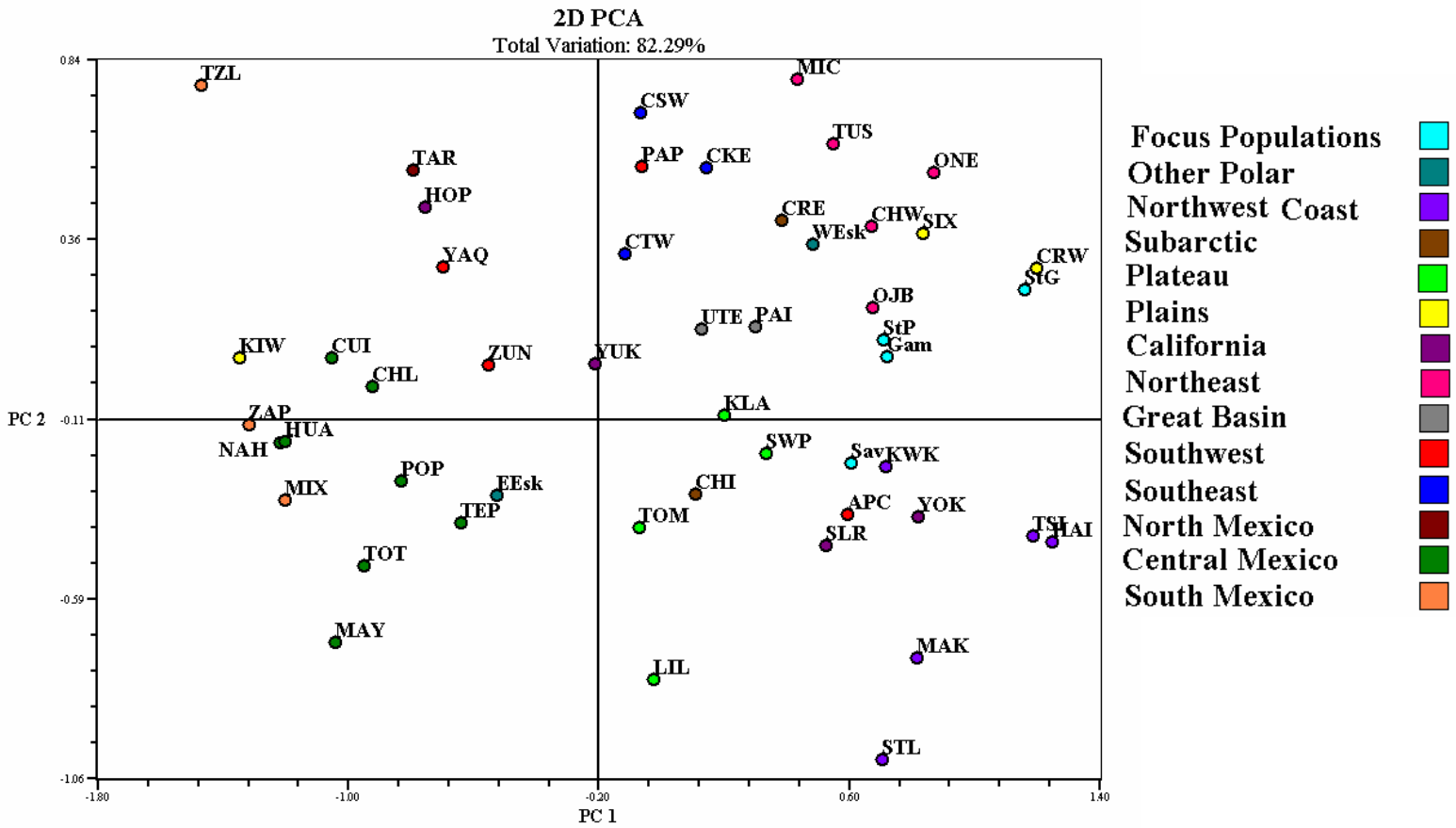
The Principal Components Analysis (PCA) using a correlation matrix demonstrated that there was only one significant component explaining the variation in the data. According to the eigenvalue test, components greater than the average are large enough to be considered significant; for a correlation matrix, this would be any component with an eigenvalue greater than 1. If we were to use this criterion alone, only the first axis would be significant enough for evaluation. However, the first three components explain much more variation than the last two; therefore, the first three components will be considered for interpretation. Table 10 outlines the eigenvectors and eigenvalues for the first three components. The first component accounts for 63.5% of the variation, and roughly separates North America from Central America with the exception of the Eastern Eskimo, Zuni, Hoopa, and Yaqui and Kiowa, which cluster with the Mesoamericans (See Figure 10). St. Paul, Gambell, and Savoonga all cluster closely along the first axis. St. George has a slightly higher score along the first component causing it to cluster closer with the Crow. This component appears to be a size component, with populations possessing the largest overall size occupying the right quadrants and populations with the smallest overall size occupying the left quadrants of the PCA plot. The second component accounts for 18.8% of variation and is a shape component contrasting

Table 10. First three eigenvectors for Principal Components Analysis.

Variable	PC1	PC2	PC3
Stature	0.7915	0.4681	0.245
Sitting Height	0.8558	0.2980	0.251
Head Length	0.7945	0.2281	-0.535
Head Breadth	0.7106	-0.6162	0.253
Bizygomatic Breadth	0.8244	-0.4474	-0.198
Eigenvalue	3.175	0.940	0.5125
Proportion	0.635	0.188	0.102
Cumulative	0.635	0.823	0.925

length and width of the body. While the first component clusters Gambell, Savoonga and St. Paul, St. Paul and Gambell are slightly closer to St. George than Savoonga on the second axis. Together, these axes represent 82.3% of the variation and fail to cluster St. Paul and Gambell closely with the other focus populations. Instead, St. George appears to be closely related to Crow, St. Paul and Gambell to Ojibwa, and Savoonga to Kwakiutl. A plot of the variables contributing to each component is given in Figure 11. This plot shows that those populations with the largest linear measurements are being pulled to the upper right quadrant. This explains why Savoonga is being pulled to the lower left quadrant, as Savoonga has the greatest bizygomatic breadth of the four study populations, and the shortest in all linear

Figure 10. Plot of the first two components of PCA representing variation among North American Natives. For other populations codes, see Table 5.



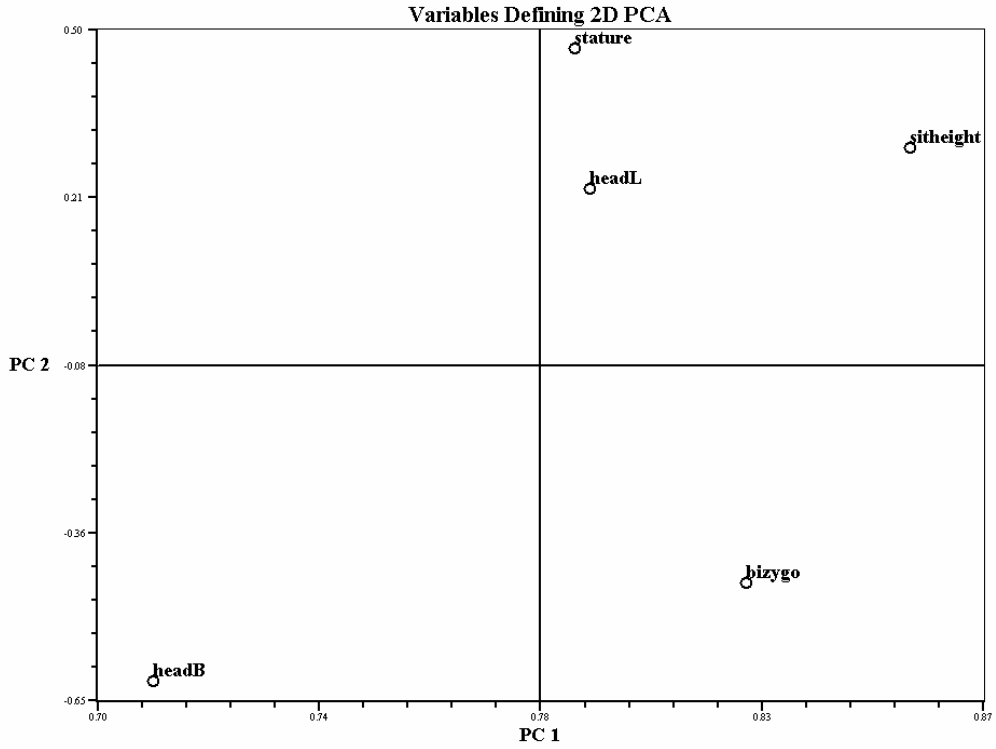
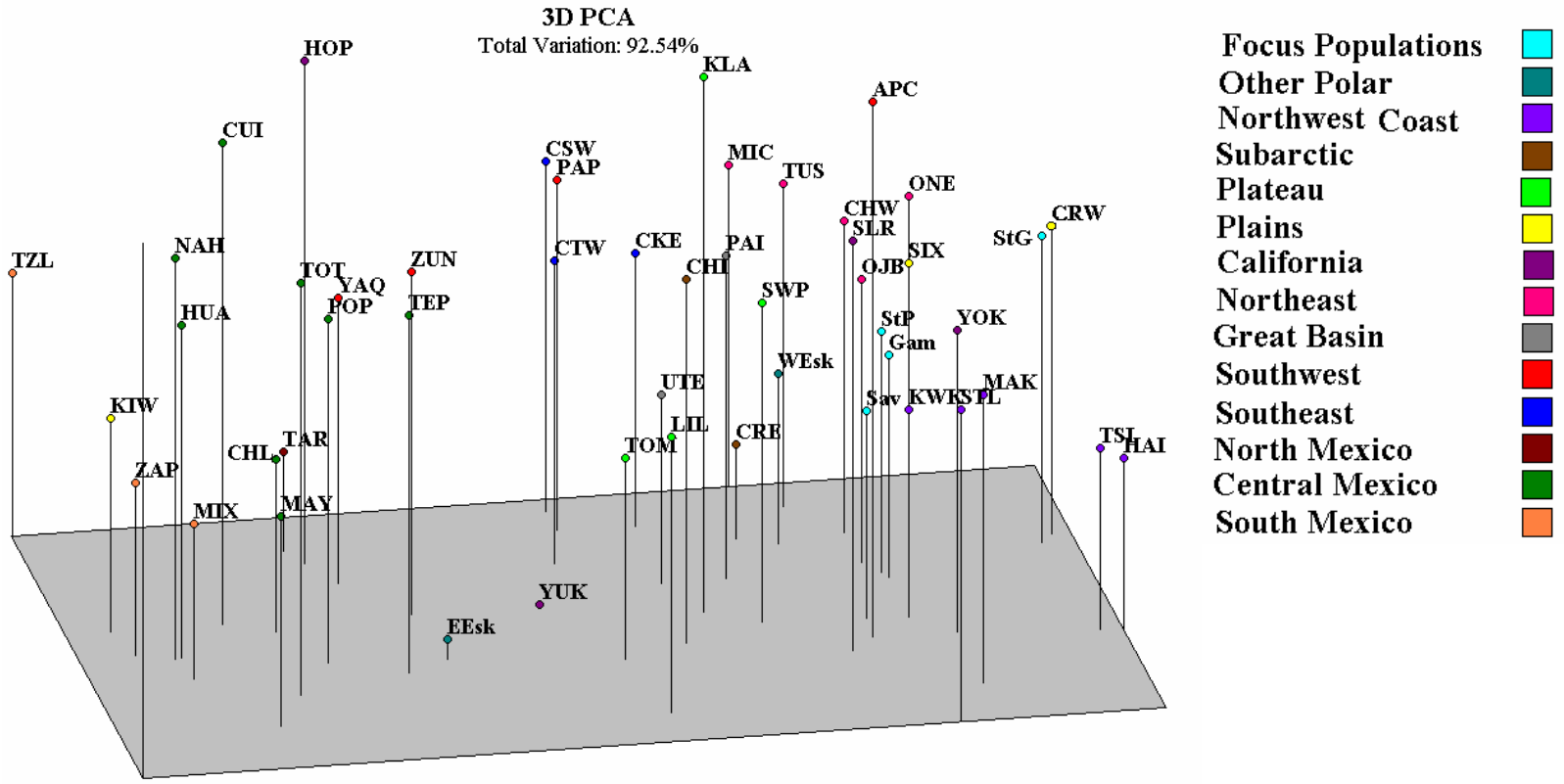


Figure 11. Plot of variables defining the 2-dimensional principal components plot.

measurements (See Table 8). This plot also stresses the contrast in the relationship between the linear measurements and the weight of head breadth. The third PC accounts for 10.2% of the variation and represents an additional shape component, contrasting height and head breadth with head length with bizygomatic breadth. On this third component, the Alaskans maintain similar trajectories along with the Western Eskimo and Kwakiutl. Savoonga is closer to St. Paul and Gambell on the third axis, than is St. George, who still clusters closely with the Crow. The

Figure 12. Plot of the first three components of PCA representing variation among North American Natives. Gambell= 2, Savoonga= 3, St. Paul= 4, and St. George= 5. For other populations codes, see Table 5.



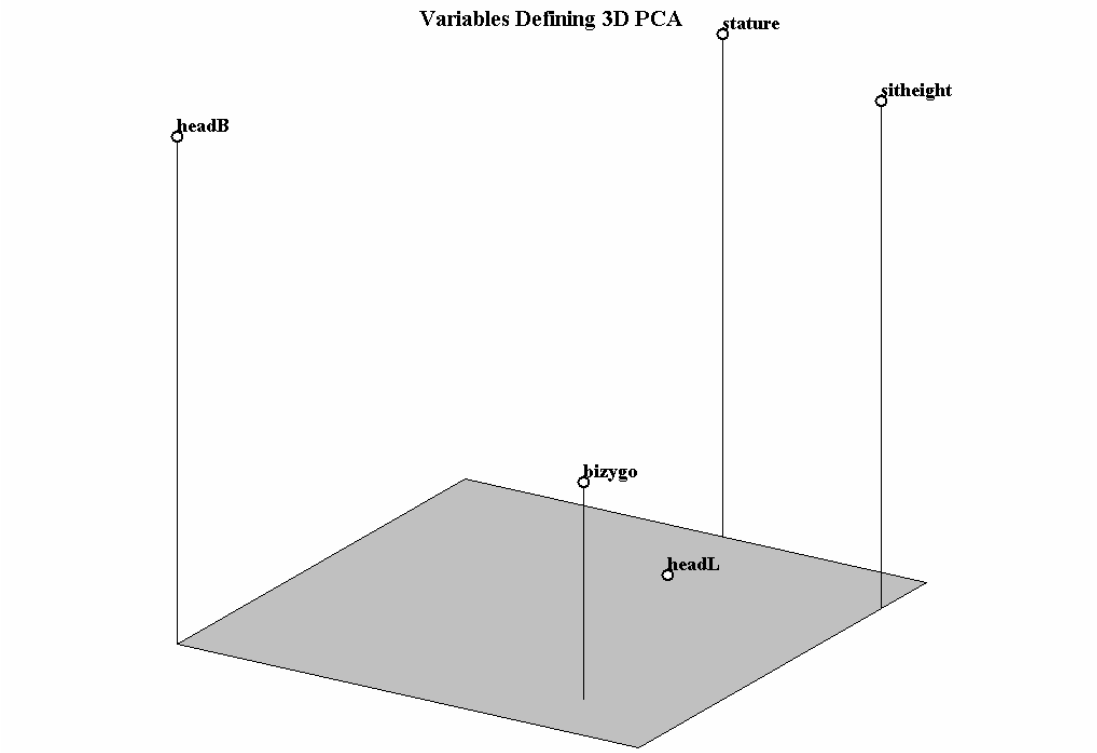


Figure 13. Variables defining the three-dimensional principal components analysis.

overall relationship between populations does not change on this component except for the Yuki and Eastern Eskimo, which now separate from the other Americans. In Figure 13, the S-matrix plot of variables highlights the contrasting relationship of head length to head breadth and the linear measurements.

For exploratory purposes, populations outside of Polar Regions were grouped and the mean from each region was used to perform a new PCA. The results of the eigenanalysis are given in Table 11. The first component accounts for 68.74% of the

variation among the regions and appears to again be explained by overall size. Similar to the analysis of ungrouped populations, Gambell, St. Paul and Savoonga cluster on the first axis (See Figure 14). All are closely related to the Western Eskimo. Contradictory to the unpooled data, the Gambell, St. Paul, and Savoonga cluster closest to the plateau and subarctic regions, while previously they clustered with members of the northeast region and Northwest Coast Indians. St. George clusters closely with the Plains Indians, likely due to their close association with the Crow. The California region clusters on the same side of the plots with the Central Americans. The second axis accounts for 14.04% of the variation and represents a shape component contrasting stature and sitting height with head measurements.

Table 11. First three eigenvectors for Principal Components Analysis on regions.

Variable	**PC1**	**PC2**	**PC3**
Stature	0.7893	0.5337	0.2549
Sitting Height	0.9158	0.2817	-0.867
Head Length	0.8617	-0.2657	0.3138
Head Breadth	0.7591	-0.0434	-0.6321
Bizygomatic Breadth	0.8102	-0.5151	0.1082
Eigenvalue	3.4368	0.7020	0.5823
Proportion	0.6873	0.1404	0.1164
Cumulative	0.6873	0.8278	0.9442

California separates from the Central Americans on this axis. All other relationships remain the same along the second axis. It is not until the third component that St. George and the northwest coast region cluster closely with the other focus populations (See Figure 15). The Western Eskimo cluster with the subarctic and southeast populations. The third component accounts for an additional 11.65% of the variation and represents and additional shape component contrasting sitting height and head breadth to the other measurements.

The Neighbor Joining Tree (NJT) roughly separates Central Americans from the other North American Natives with few exceptions. Therefore, for ease of viewing, these branches are shown in two separate figures (Figure 16 and 17). In the NJT of Northern North Americans Gambell, Savoonga, and St. Paul all cluster together on a branch with the Kwakiutl (marked as node 1 on Figure 16), similar to the relationships shown in the PCA. Savoonga and Kwakiutl are OTUs on a single branch as are St. Paul and Gambell. St. George is again clustering with the Crow on node 2. Also, node 2 contains all of the East Coast Native Americans and Plains Indians, except the Kiowa, which cluster with the Central Americans. The branch marked as node 3 contains all West Coast Indians, with the sub-branch marked node6 clustering all Northwest Coast Indians exclusive of the Kwakiutl, which cluster with the focus populations. The Eastern Eskimo cluster with the Yuki, a Central California population, and represent the most divergent node among the northern North Americans. As shown by node 5, the Eastern Eskimo are intermediate between the Central Americans and other North Americans.

Figure 14. Plot of the first two components of PCA representing variation among geographical regions of North American Natives. For other populations codes, see Table 8.

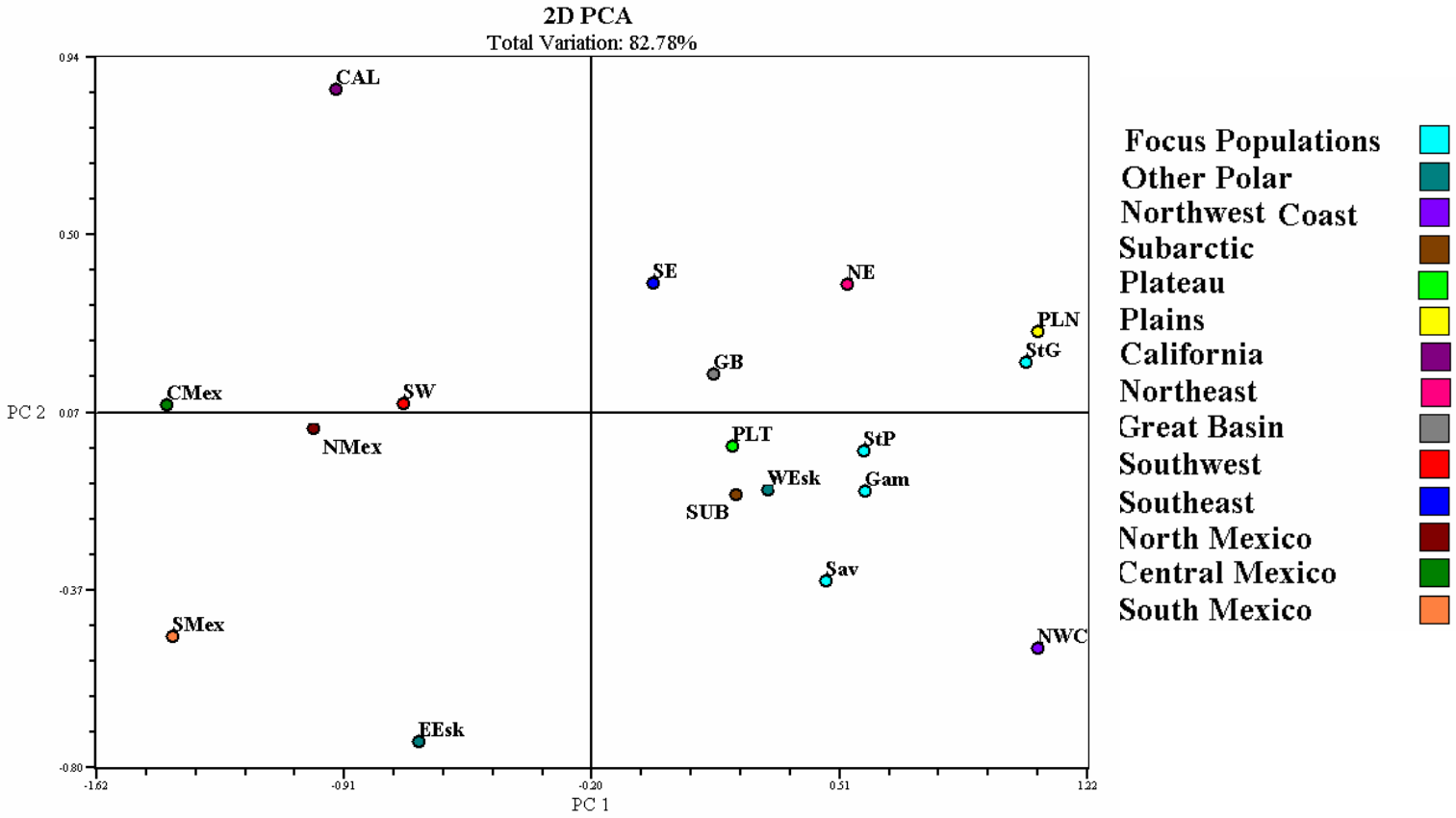
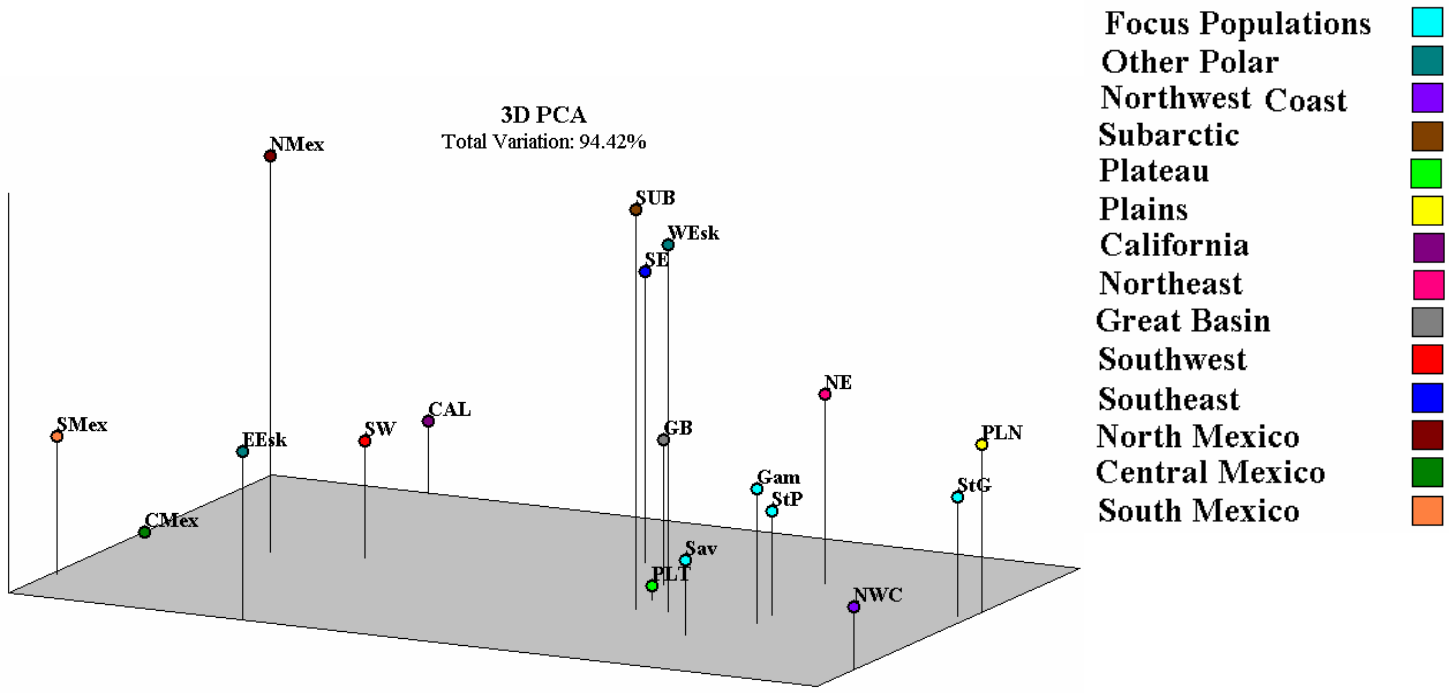


Figure 15. Plot of the first three components of PCA representing variation among geographical regions of North American Natives. For other populations codes, see Table 5.



Similar to the PCA, the Kiowa and Hoopa cluster with the Central Americans. Addiitonally, two of the Southwest populations, Zuni and Yaqui, share branches with Central American Natives (See Figure 17). It is not surprising that the Yaqui cluster with the Central Americans, as they migrated to the southwest from Northern Mexico after the Spanish arrived in Mexico. All Central Mexicans cluster together in node 7. It is surprising that the Hoopa cluster closely with the Tarahumara and Tzotzil (node 8), as all of these populations are geographical distance. However, the Hoopa tend to have shorter stature, smaller overall body size, and a narrow face (See Table 8) when compared to other northern North Americans, as do the Tzotil and Tarahumara. Similar to the PCA, the Kiowa cluster with the Zapotec and Mixtec, likely due to their overall small body size (node 9).

A Mantel randomization test was performed comparing a cophenetic matrix created from the Neighbor Joining Tree and the original Euclidean distance matrix. The test revealed a correlation of 0.6674, with a $p=0.0007$. Although there is a significant correlation between the two, it is not strong. Because of the loss of information when converting a matrix into a tree representation, the Neighbor Joining Tree may not be the best method to examine the relationship among Native Americans. Again, one would assume that if the comparative data set were increased to include other North American and Siberian populations, then the Neighbor Joining Tree would increase in accuracy.

Figure 16. Neighbor-joining tree created from Euclidean distance matrix showing the phylogenetic relationship among American Indians.

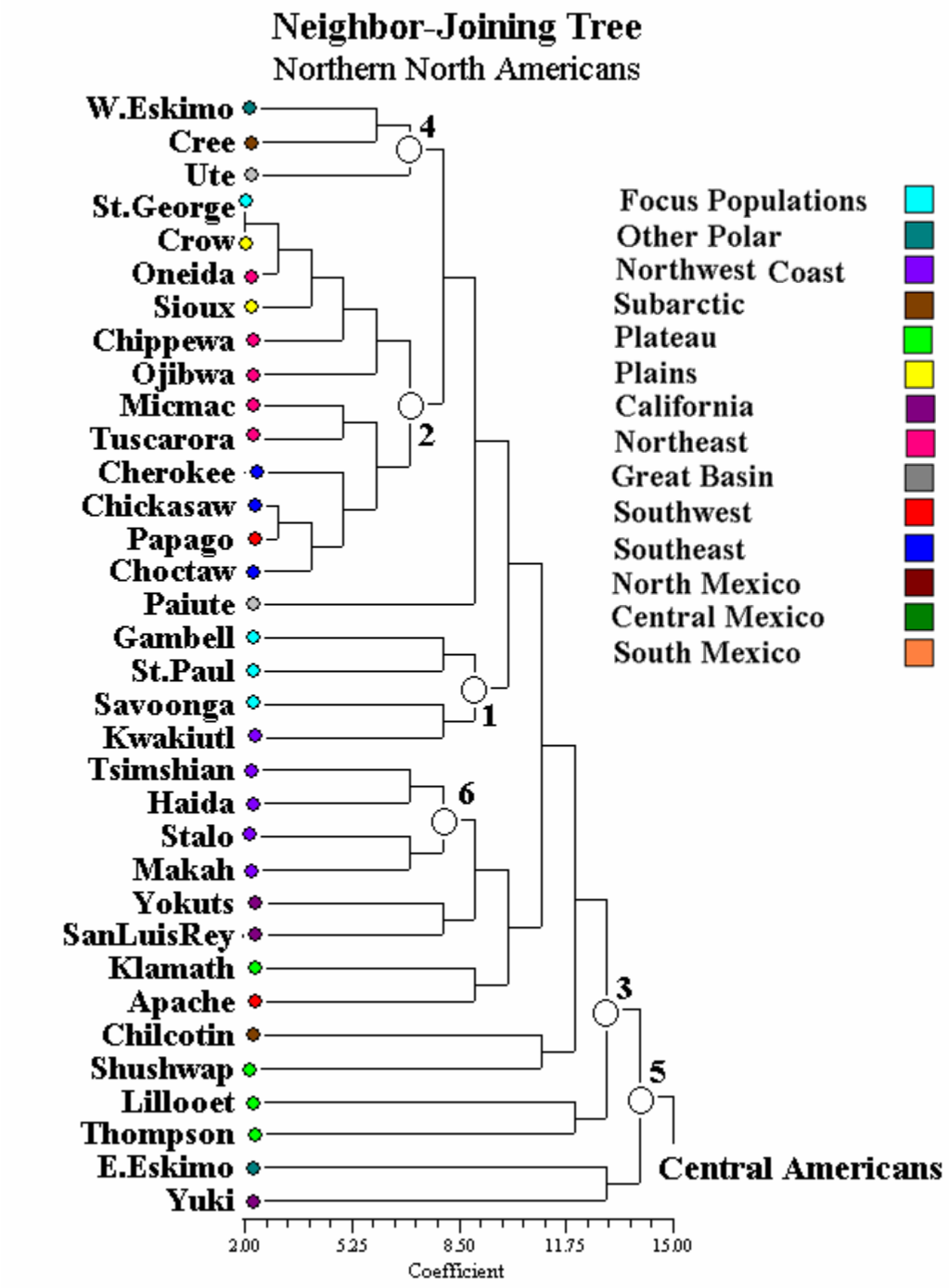
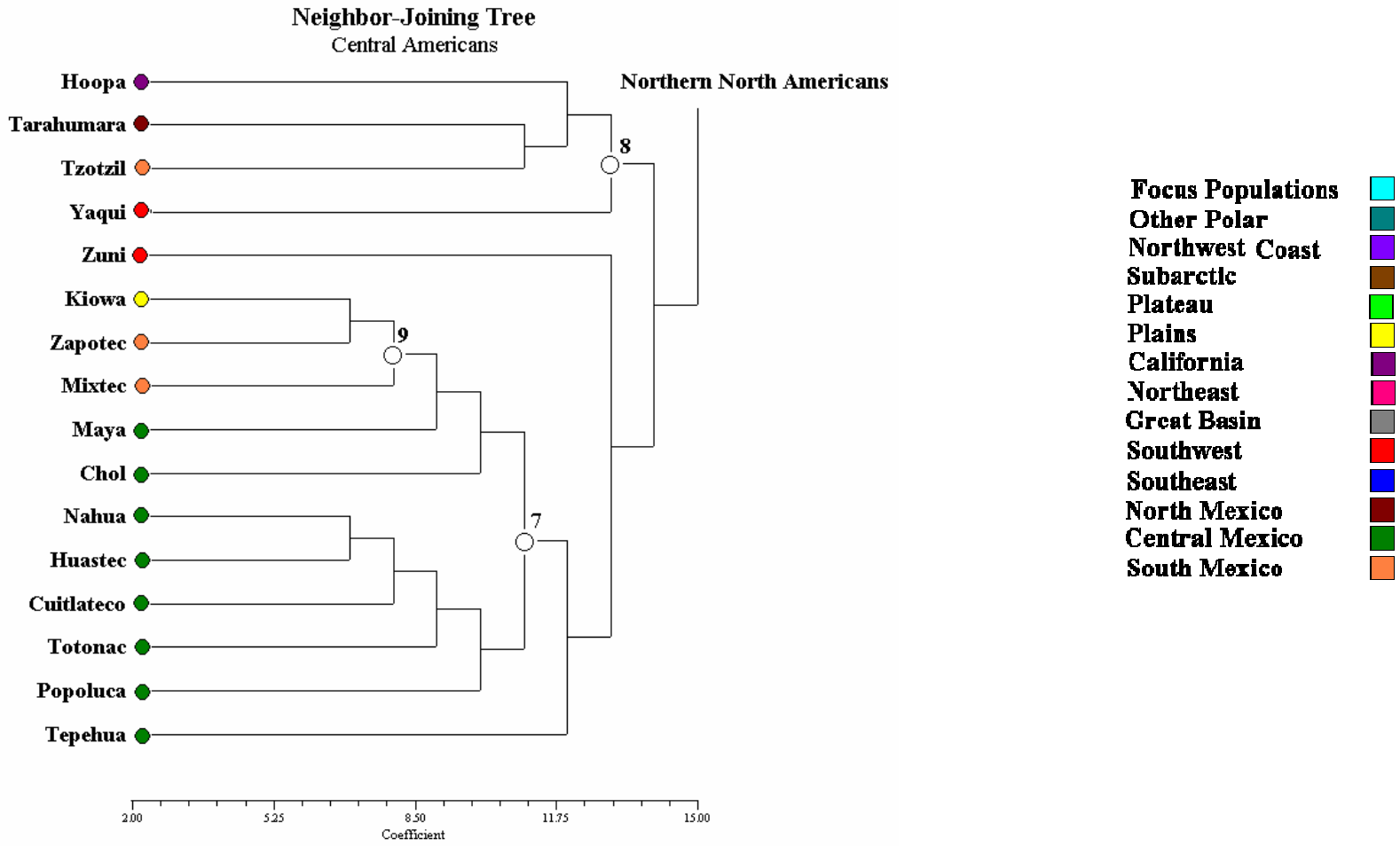


Figure 17. Neighbor-joining tree created from Euclidean distance matrix showing the phylogenetic relationship among American Indians.



CHAPTER 6: DISCUSSION

I. Bering Sea Natives

It is important to note that while this study revealed morphological similarity between Aleuts and Eskimos in the Bering Sea, this relationship may be distorted by the influence of environmental pressures on anthropometric traits. In addition, this relationship may be affected by natural selection. The time difference between the measurements of populations may have an effect on the data, possibly as a result of secular trends related to improved nutrition and/or better healthcare. Some differences between populations may reflect temporal distance rather than genetic distance. However, in previous studies of Tlaxcaltecan populations, no significant difference has been found in temporally distant samples collected in 1969 compared to those collected by Starr in 1905 (Lees and Crawford 1976). While inter-observer error is not an issue for the primary data being discussed, and thus should not affect our interpretation of relations among Aleuts and St. Lawrence Eskimos, it may be a concern with the comparative samples. All measurements for Pribilofs and St. Lawrence Islands were taken by WS Laughlin himself. However, Boas utilized 50 different anthropometric specialists with standardized methods of collection to gather measurements. Many early anthropologists understood the importance of standardizing the collection of data, and Boas especially tried to limit error as much as possible (Jantz 2006). On the other hand, many of the Middle American data sets were collected by individual investigators, with no standardized methodologies

defined. Despite differences in time of data collection, many of our results confirm previous findings in which the data set did not span a large time frame, as discussed below (Ousley 1995, Jantz et al 1992).

The correlation between anthropometrics and immunological markers may have been affected by the comparative samples used in this study. All individuals claiming non-Aleut ancestry were excluded from Majumder et al (1988). Estimates based on mitochondrial DNA halpogroups show 10.5% of non-Aleut native (primarily Athapaskan) admixture into St. Paul and 0.07% of European admixture (Rubicz et al 2003). Also, 90% of the male lineages in St. Paul are non-native, while 89% of St. George and 87% of Aleutian male lineages are non-native (Rubicz 2007). Of the two Pribilof communities, St. Paul was responsible for three fourths of the fur seal hunting, and job opportunities in the fish-packing plant, thus attracting immigration (Ropell and Davey 1965). In 1970, only 7 individuals from St. George were reported as being non-native, while 22 St. Paul reported the same (Lantis 1984). Therefore, the exclusion of these individuals would have the greatest influence on the relationship between St. Paul and the other populations, especially Gambell. With these considerations in mind, it is not surprising that the correlation between immunological markers and anthropometrics would not be significant.

The application of the Relethford-Blangero method revealed differences in the variability of physical traits between males and females. Males overall have a higher average within-group variation (see Appendix A and B). Most of this variability can be attributed to the sample from St. George. The variation in St. George for the males

and the population considered as a whole deviates in a visibly positive pattern, likely due to admixture. Savoonga, has higher variability in anthropometric traits than does Gambell. Gambell was used as a military (airforce) base during World War II and has experienced recent admixture with Europeans. These factors have resulted in Gambell having the greatest amount of European gene flow (8.1%) as measured by blood markers (Byard et al 1983). Despite these facts, Savoonga possesses higher within-group variation than Gambell, and both lower than either Aleut population. This is likely a consequence of Savoonga being founded by the younger generation from Gambell, possibly representing a kingroup migration. This results in Savoonga having a large breeding population relative to the total population, and thus undergoing an expansion within the few generations following the migration, but with less European admixture than Gambell. European admixture for Savoonga based on immunological markers has been estimated as 4.3% (Byard et al 1983). Byard and Crawford (1991) also found that when using blood group immunoglobulin markers, despite the smaller effective population size of Gambell, there was no difference between expected and observed heterozygosity. They did find that heterozygosity was reduced when only comparing "native" Eskimos. Our results conform to the expectation of reduced variation in Gambell due to restricted effective breeding size as seen in classical genetic markers. The females of Gambell have the least amount of variation of all populations considered (see Appendix B). Savoonga's phenotypic variation is slightly higher for females than Gambell. This is likely a result of men importing Siberian wives to Savoonga after males split from Gambell to become reindeer herders

(Crawford et al 1981). It is also important to note that Gambell is consistently the closest to the mean as evidenced by its low r_{ii} values across all tests. However, Gambell is also the least heterozygous using classical markers (Byard et al 1983) and in morphological variability (this study). These results are consistent with studies performed on Mennonite populations of Kansas, in which no correlation between heterozygosity and morphological variation was detected (Commuzzie and Crawford 1990). The findings of these two studies thus deviate from the expectation, "For a trait controlled by polygenes individuals most proximal to the population mean are the most heterozygous for that trait. Such a relationship between heterozygosity and phenotypic distribution is a reflection of the additive nature of loci in a polygenic system" (Comuzzie and Crawford 1990: 101). This study did show a few correlations between individual heterozygosity and morphological variation, but these correlations were sex specific and only significant results were found in females. These results put into question the combined relationship between classical markers, morphology and actions of homoestasis.

Despite a longer history of occupation on St. Lawrence Island, it appears that recent demographic events have had a greater negative effect on the phenotypic variation of St. Lawrence Eskimos when compared to Pribilof Islands Aleuts. This may also be the result of the parental populations of St. Paul and St. George being from multiple islands, thus giving the Pribilofs an increased amount of variation to start with (Rubicz 2007). Also, the great famine and disease that decimated St.

Lawrence Island from 1878-1920 may have caused a bottleneck effect reducing the variation on the island.

Similar relationships are noted among the Aleut populations. In this case, St. Paul has experienced greater recent male immigration (90% non-native male lineages) as compared to St. George (89% non-native Y) (Rubicz 2007), but males have lower variation than that found within St. George. Similarly, the females of St. Paul have less variability than do females of St. George. When males and females are examined together, St. George exhibits the greatest positive deviation from expectation. Gambell and St. Paul had close to the same population size at time of collection, but Gambell has probably experienced less gene flow than has St. Paul, and the smaller effective population size made Gambell more subject to affects of genetic drift. St. Paul and St. George have also had an increasing number of non-Aleuts entering the region, due to easier access of the islands through commercial air travel and the promise of employment in the crabbing and fishing industries.

It is clear from the deviation from expected within-group variation for the Aleut and Eskimo populations that famine, relocation and admixture have had an effect on their genetic structure. These patterns are also discernable within the R-matrices and PCA results. In all R-matrices, Savoonga clusters with Gambell as does St. Paul with St. George showing the similarity within each group, and morphological differences between Aleuts and Eskimos. On the second axis of all of these tests, and on the PCA plots, St. Paul and Gambell cluster together. This is indicative of Russian and European-American gene flow into Gambell and St. Paul. Both of these

populations have tended not to increase in size as quickly as their counterparts, while accumulating non-native gene flow.

Changing the variables with which the R-matrices were generated also lent insight into the relationships among these populations. When using a model including only the four indices, St. Paul showed the highest positive deviation from expected variance. This deviation can be explained by the following: 1) either this is also a remnant of admixture in which the male gene flow has resulted in changes in body proportions such as longer limb length; 2) evidence of a secular trend created by changes in diet that began upon their return to the island after WWII; or 3) a result of recent population expansion in addition to admixture. The first two explanations are unlikely considering their average indices are similar to the other populations. The deviation is more likely the result of an increase in population size. Including the indices with the other twelve variables reduces the estimates of population substructure which coincides with previous findings of these body proportions (especially stature/sitting height) being highly conserved among these populations (Laughlin 1980) as a result of climatic pressures. They have a long torso and relatively short limbs as expressed in their average ratio of 0.544 for sitting height/stature.

The PCA plots provide additional insight into the relationship among the Alaskan natives. In all plots, St. George is the most morphologically distinct population and does not cluster as closely with the other Bering Sea natives. As mentioned previously (see pages 63 and 64), all R-matrices presented in this study

were scaled by the population census sizes. This scaling diminishes the effects of genetic drift on variation within populations, allowing the investigator to infer past relationships that are not affected by stochastic processes, i.e. gene flow (Relethford 1996). For most of the R-matrix analyses, this scaling results in only minor differences for the overall relationship between the Bering Sea populations; however, when only using the four indices, these differences become pronounced (Figure 6). In this case, the unscaled R-matrix reveals that St. George does not cluster closely with any of the other Alaskan natives, the same pattern present in the PCA plots. This and the large r_{ii} values for males from St. George and males and females combined is suggestive of changes in morphological variation due to genetic drift.

St. George is relatively isolated from immigration, but has the greatest amount of anthropometric variation among the Aleuts under study, and does not cluster closely with either of the Eskimos and St. Paul on the PCA plots. St. George did increase in size faster in relation to St. Paul, which may increase variation. St. George has less male European gene flow than does St. Paul, and much less mtDNA diversity (Rubicz 2007). Therefore, one could assume that St. George differs from the others due to lack of European admixture. However, St. George had the highest frequency of RH cde (0.161), considered a European marker. Furthermore, previous studies have shown that genetic variation may not be highly correlated with gene flow if there are multiple forces of evolution operating on small populations (Byard et al 1983). Based on morphology, St. George has the greatest stature among the Bering Sea natives in both males and females, clusters with the Crow in the PCA plots and shares a

common branch of the dendrogram with the Crow on the NJT. While St. George has the highest mean stature among Aleuts and Eskimos, the Crow have the highest mean stature across all populations in the study. So, while the results of the Relethford-Blangero analysis do not reveal substantial non-native admixture, other analyses offer an alternative interpretation. Based on the analysis of blood group markers (Majumder et al 1988) and results of the PCA and NJT on anthropometrics, it is likely that St. George has had a significant amount of Russian and European-American gene flow, which resulted in greater changes in physique due to genetic drift. Therefore, due to the confounding effects of small population size and gene flow, St. George has differentiated from St. Paul and the St. Lawrence Island Eskimos, and appears to be morphologically similar to the Crow Indians.

II. Bering Sea Native and other North American Natives

St. George is projected further from the Middle Americans on the two-dimensional PCA plots, likely due to their stature and overall larger size. St. Paul and the St. Lawrence Island Eskimo tend to form a cluster along with Native Americans from the Northwest and Northeast Coasts and Western Eskimo. This would seem to lend itself to the previous assumptions regarding environmental pressures associated with Bergman's and Allen's Rules and relationship among the Native Americans. However, the NJT showed an alternative relationship, roughly grouping western Natives together and Eastern natives together. Geographic distance in latitude showed little correlation to anthropometric distance among Northern American Natives in the Mantel tests. Previous studies have also found a pattern of relationship from West to

East (Jantz 2006), which would be expected if a single migration moved down the West Coast and populated the United States from West to East. Again, the Mantel tests revealed no significant relationship between longitude and anthropometric distance for populations North of Mexico. However, the relationship between longitude and phenotypic variation may be affected by a higher concentration of European admixture in the East. A secular trend of increased height and increased leg length has been noted in the eastern United States (Jantz 2006). The tests showing a relationship between anthropometrics and longitude used Boas's data, grouped into major geographical regions, and incorporated a more complete set of populations than found in the current study. These factors may have influenced our findings. Cavalli-Sforza et. al. (1994) detected a similar pattern of inter-population variation in the Northeast when examining genetic markers, which he attributed to the colonization of North America and the movement of Europeans into the West.

The Eastern Eskimo were the most divergent of the northern North American populations on the NJT, and failed to cluster with the other polar populations on the PCA as well. This may be due a combination of a more distant phylogenetic relationship with the other Eskimo-Aleuts and differential gene flow. While the Eastern Eskimo have undergone European-American admixture, estimates using both mtDNA and Y-chromosome data indicate far less than that found in the Aleuts. Bosch et al (2003) found only 58% of the Y-chromosome lineages came from European gene flow in Greenlandic Eskimos compared to estimates of 73-90% for Aleut populations (Rubicz 2007).

While there is a close relationship between the Savoonga and the Kwakiutl, there does not seem to be a strong relationship between the Northwest Coast Indians and the Bering Sea natives when the populations are grouped by region in the PCA plots. On the other hand, the NJT would seem to support a strong relationship between Aleuts, Eskimos, and all west coast populations including some southern Californian populations. Therefore, the pooling of populations by region may be misleading.

The current estimate for population substructure among the Aleuts and Eskimos is far lower than any estimate of F_{st} using Boas' data (This study = 0.0420, Siberia = 0.12, Aleut and NW Coast = 0.27, NW Coast only = 0.26) (See table 7, Ousley 1995). This is indicative of the strong phylogenetic relationship between Aleuts and Eskimos resulting in little phenotypic variation. However, as mentioned earlier, heritability may be higher in populations living in extreme environments, in which case, the estimates of F_{st} may decrease (See pages 63 and 64 for further discussion).

CHAPTER 7: CONCLUSIONS

Despite confounding difficulties due to inter-observer error, and temporal distance in sampling, all tests reveal a close phylogenetic relationship between St. Lawrence Island Eskimos and Pribilofs Islands Aleuts. Several other studies based on genetic and archaeological evidence support the same conclusions, in which Alaskan Yupik Eskimos and Aleuts exhibit strong affinities to one another and with North Pacific Amerindians.

St. George is the most divergent of the four focus populations. This is likely due to St. George having had a significant amount of Russian and European-American gene flow combined with genetic drift. Therefore, due to the confounding effects of small population size and gene flow, St. George has differentiated from St. Paul and the St. Lawrence Island Eskimos. While they appear to be morphologically similar to the Crow Indians, this does not reflect a phylogenetic relationship. Despite large amounts of European gene flow and other Native American gene flow as a result of adoption, Gambell's small effective breeding population has resulted in restricted variability. Conversely, mating patterns in Savoonga combined with larger effective breeding size have resulted in greater within-group phenotypic variance as compared to Gambell.

Body proportions are conserved among the St. Lawrence Island Eskimos and Pribilofs Aleuts. These body proportions mimic the expectations of Bergman and Allen's rule for greater body volume to surface area. However, while this pattern

exists here, there was no notable correlation found between latitude and morphology outside of the northwest arctic. The only clearly discernable relationship to geography is seen in the separation of North and Central Americans. However, geography plays a more important role in determining anthropometric distance in Central Americans rather than Northern Americans.

Similar to other findings, Aleuts and Yupik Eskimos have a close phylogenetic relationship with Northwest American Indians. Additionally, this thesis revealed a closer relationship to other Western populations in the NJT and Northeastern populations in the PCA. However, Eastern Eskimo in this study clustered among the Mesoamericans. In previous studies, the Eastern Eskimo clustered with Siberian populations (Ousley 1995, Jantz et al 1992), which were not used in this analysis, likely causing the unexpected pattern of Eastern Eskimo relationships. These results would also explain the discreapancy between previous studies which found little relationship between Aleuts and Eskimos as only Inupik Eskimos were used for comparison, but a greater relationship exists among Aleuts and Yupik-speaking Eskimos. Other studies which include Yupik Eskimos produced similar results with data collected over shorter period of time. Therefore, the results of this study provide evidence that secular trend has not impacted these native populations, even though data collection occurred over seven decades between Boas' and Laughlin's expeditions. These results highlight the complicated relationship among North American Natives residing in the United States and Canada, as noted elsewhere (Jantz et al 1992). The lack of fit to geography indicates that the physique

of these populations has been affected by a combination of migration and non-native gene flow. Central America seems less affected by these factors, thus maintaining a closer resemblance in morphological traits.

This study supports claims that environmental plasticity is not great enough to obscure relationships among populations due to population history. In line with previous studies, these results challenge Boas' original claims concerning the magnitude and influence of plasticity on anthropometric traits (Sparks and Jantz 2002, Gravlee et al 2003, Relethford 2004, this study).

As studies have shown in recent publications, multivariate methods can be applied to anthropometrics and used to infer population history and substructure (Gonzalez-Jose et al 2007, Nystrom 2006, Relethford and Blangero 1990, Relethford et al 1997, Relethford and Harpending 1994, Scherer 2007, Jantz 1995, Jantz and Owsley 2001, Jantz 2006, Ousley 1995, Sparks and Jantz 2002, Williams-Blangero and Blangero 1989). Our results show a relationship linking geography, history and underlying genetic relationship of the Amerindian populations.

BIBLIOGRAPHY

Black L (1983) Some problems in the interpretation of Aleut prehistory. Arctic Anthropology 20(1):49-78.

Bonatto S, and Salzano F (1997) A single and early migration for the peopling of the Americas supported by mitochondrial DNA sequence data. Proc Natl Acad Sci U S A 94:1866-71.

Bosch, E, F Calafell, ZH Rosser, S Nørby, N Lynnerup, ME Hurles, MA Jobling (2003) High level of male-biased Scandinavian admixture in Greenlandic Inuit shown by Y-chromosome analysis. Human Genetics; 112 (4): 353-363.

Byard P (1981) Genetics of the St. Lawrence Island Eskimos. Unpublished dissertation, University of Kansas, Lawrence, Kansas.

Byard P, Schanfield M, and Crawford MH (1983) Admixture and heterozygosity in West Alaskan populations. Journal of Biosocial Science 15:207-216.

Byard P and Crawford MH(1991)Founder effect and genetic diversity on St. Lawrence Island, Alaska. HOMO 41(3):219-227.

Cavalli-Sforza LL, P Menozzi, and A Piazza (1994) The History and Geography of Human Genes. Princeton University Press: Princeton, NJ.

Collins, HB (1937) Culture migrations and contacts in the Bering Sea Region. American Anthropologist, New Series, Vol. 39, No. 3, Part 1. (Jul. - Sep., 1937), pp. 375-384.

Collins H (1964) The Arctic and Subarctic. In: Prehistoric Man in the New World, ed by J. Jennings and E. Norbeck, University of Chicago Press: Chicago.

Coltrain, J. B., M. Geoffrey Hayes, and D. H. O'Rourke (2006) Hrdlicka's Aleutian population replacement hypothesis: A Radiometric evaluation. Current Anthropology 47:537-548

Comuzzie, AG, MH Crawford (1990) Biochemical heterozygosity and morphological variability: interpopulationsl versus intrapopulational analyses. Human Biology; 62 (1): 101-112.

Crawford MH, JH Mielke, EJ Devor, DD Dykes, and HF Polesky (1981) Population structure of Alaskan and Siberian indigenous communities. American Journal of Physical Anthropology 55(2): 167-186.

Crawford, MH, JT Williams, R Duggirala. (1997) Genetic structure of the indigenous populations of Siberia. American Journal of Physical Anthropology; 104: 177-192.

Crawford, MH. (2007) Genetic structure of circumpolar populations: A synthesis. American Journal of Human Biology; 19: 203-217.

Crawford MH (1998) The Origins of Native Americans: Evidence from anthropological genetics. New York: Cambridge University Press.

Derbeneva, OA, RI Sukernik, NV Volodko, SH Hosseini, MT Lott, and DC Wallace. (2002) Analysis of mitochondrial DNA diversity in the Aleuts of the Commander Islands and its implication for the genetic history of Beringia. American Journal of Human Genetics; 71: 415-421.

Devor EJ, McGue M, Crawford MH, Lin PM (1986a) Transmissible and nontransmissible components of anthropometric variation in the

Alexanderwohl Mennonites: I. Description and familial correlations. American Journal of Physical Anthropology. 69(1):71-82.

Devor EJ, McGue M, Crawford MH, Lin PM (1986b) Transmissible and nontransmissible components of anthropometric variation in the Alexanderwohl Mennonites: II. Resolution by path analysis. American Journal of Physical Anthropology. 69(1):83-92.

Dumond, Don E. (1977) The Eskimos and Aleuts. London, Thames and Hudson.

Dumond, Don E. (2001) Toward a (Yet) Newer View of the (Pre)History of the Aleutians. In Don E Dumond (ed.): Archaeology in the Aleut Zone of Alaska, University of Oregon Anthropological Papers 58. Department of Anthropology and Museum of Natural History, University of Oregon: 289-309.

Faulhaber J (1970) Anthropometry of Living Indians. In R Wauchope (ed.): Physical Anthropology. Austin: University of Texas Press, pp. 296.

Ferrell R, Chakraborty R, Gershowitz H, Laughlin W, and Schull W (1981) The St. Lawrence Island Eskimos: Genetic variation and genetic distance. American Journal of Physical Anthropology 55:351-358.

Forbes, JD (1957) Historical Survey of the Indians of Sonora, 1821-1910. Ethnohistory v4,4:335-368.

Gonzalez-Jose R, Martinez-Abadias N, Gonzalez-Martin A, Bautista-Martinez J, Gomez-Valdes J, Quinto M, and Hernandez M (2007) Detection of a

population replacement at the Classic-Postclassic transition in Mexico. Proc Biol Sci 274:681-8.

Gravlee CC, HR Bernard, WR Leonard (2003) Heredity, environment, and cranial form: a reanalysis of Boas's immigrant data. American Anthropology 105: 125-138.

Greenberg J, Turner C, and Zegura S (1985) Convergence of evidence for the peopling of the Americas. Collegium Anthropologicum 9:33-42.

Harpending HC, Ward (1982) Chemical systematics and human evolution. In M Nitecki (ed.): Biochemical Aspects of Evolutionary Biology. Chicago, IL: University of Chicago Press.

Harper, AB. (1980) Origins and divergence of Aleuts, Eskimos, and American Indians. Annals of Human Biology; 7 (6): 547-554.

Hayes, MG. (2002) Paleogenetic assessments of human migration and population replacement in North American arctic prehistory. Unpublished Dissertation, University of Utah, Utah.

Helgason A, G. Pálsson, HS Pedderson, E Angulalik, ED Gunnarsdóttir, B Yngvadóttir, and K Stefánsson. (2006) mtDNA variation in Inuit populations of Greenland and Canada: migration history and population structure. American Journal of Physical Anthropology; 130: 123-134.

Holland, Kathryn M. (2001) Regional Interaction as seen from the Eastern Aleutians. In Don E Dumond (ed.): Archaeology in the Aleut Zone of Alaska, University

of Oregon Anthropological Papers 58. Department of Anthropology and Museum of Natural History, University of Oregon: 173-182.

Hughes C (1984) Saint Lawrence Island Eskimo. In: Handbook of North American Indians, Vol 5 Arctic. Smithsonian Institution: Washington. 262-277.

Jantz, RL, DR Hunt, AB Falsetti, and PJ Key (1992) Variation among North Amerindians: Analysis of Boas's anthropometric data. Human Biology. 64(3): 435-461.

Jantz, RL (1995) Franz Boas and Native American biological variability. Human Biology. 67(3): 345-354.

Jantz, Rl and DW Owsley (2001) Variation among early North American crania. American Journal of Physical Anthropology. 114(2): 146-55.

Jantz, Richard L. (2006) Anthropometry. In: Handbook of North American Indians. D Ubelaker (ed). Vol 3 Environment Origins and Populations. 777-788.

Jobling M, Hurles M, and Tyler-Smith C (2004) Human evolutionary genetics: origins, peoples & disease. New York: Garland Science.

Johnston, FE, LM Schell. (1979) In, *Origins and Affinities of the First Americans.* W.S. Laughlin and A.B. Harper (eds.), Gustav Fisher, N.Y., pp. 275-291. 1979.

Johnston FE, Laughlin WS, Harper AB, and Ensroth AE (1982) Physical growth of St. Lawrence Island Eskimos: body size, proportion, and composition. Am J Phys Anthropol 58:397-401.

Knecht, Richard A. and Richard S. Davis (2001) A Prehistoric Sequence for the Eastern Aleutians. In Don E Dumond (ed.): Archaeology in the Aleut Zone of Alaska, University of Oregon Anthropological Papers 58. Department of Anthropology and Museum of Natural History, University of Oregon: 269-288.

Kolhoff D (1995) When the Wind was a River, Aleut Evacuation in World War 11. University of Washington Press: Seattle and London.

Konigsberg, Lyle W. and Stephen D. Ousley. (1995) Multivariate quantitative genetics of anthropometric traits from Boas Data. Human Biology 67, 3: 481-498.

Lalueza-Fox C, Calderon FL, Calafell F, Morera B, and Bertranpetit J (2001) MtDNA from extinct Tainos and the peopling of the Caribbean. Ann Hum Genet 65:137-51.

Lantis M (1984) Aleut. In: Handbook of North American Indians, Arctic Vol. 5. Ed by D Damas, Smithsonian Institution: Washington, pp. 161-184.

Laughlin, WS (1951) The Alaska Gateway viewed from the Aleutian Islands. In: Papers on the physical anthropology of the American Indian. New York: The Viking Fund, Inc.

Laughlin, WS (1975) Aleuts: Ecosystem, Holocene history, and Siberian origin. Science; 189(4202): 507-515.

Laughlin WS and Harper AB, eds (1979) The First Americans: Origins, Affinities and Adaptations. New York: Gustav Fischer.

Laughlin W (1980) Aleuts: Survivors of the Bering Land Bridge. Holt, Reinhart and Winston: New York.

Lees, FC and MH Crawford (1976) Anthropometric Variation in Tlaxcaltecan populations. In: The Tlaxcaltecans: Prehistory, demography, morphology, and genetics. Ed by MH Crawford, University of Kansas Publications: Lawrence, Kansas.

Leffell, MS, MD Fallin, HA Erlich, M Fernandez-Vina, WH Hildebrand, SJ Mack, and AA Zachary. (2002) HLA Antigens, alleles and haplotypes among Yup'ik Alaska natives; report of the ASHI Minority Workshops, Part II. Human Immunology; 63(7): 614-625.

Madrigal L, A Ritzheimer, M Blell, A Justice. 2003. The portrayal of human bone marrow variation by the media: An important public role for human biologists. American Journal of Human Biology. 15:2 (272-273).

Majumder P, Laughlin W, and Ferrell R (1988) Genetic variation in the Aleuts of the Pribilof Islands and the Eskimos of Kodiak Island. American Journal of Physical Anthropology 76:481-488.

McDonald, JD (2005) Internet Source <http://www.scs.uiuc.edu/~mcdonald/WorldHaplogroupsMaps.pdf> Accessed November 28, 2007.

Merriwether D, Rothhammer F, and Ferrell R (1995) Distribution of the four founding lineage haplotypes in Native Americans suggests a single wave of migration for the New World. American Journal of Physical Anthropology 98:411-430.

Merriweather DA, and Kaestle FA (1999) Mitochondrial Recombination (Continued?). Science 285:837.

Minitab, Inc. (1998) Minitab for Windows v. 12.1. Computer Software.

Moscoso J, MH Crawford, JL Vicario, M Zlojutro, JI Serrano-Vela, R Reguera, and A Arnaiz-Villena (2007) HLA genes of Aleutian Islanders living between Alaska (USA) and Kamchatka (Russia) suggest a possible Southern Siberia origin. Molecular Immunology. In print.

Nystrom, KC (2006) Late Chachapoya Population Structure Prior to Inka ConqueSt. American Journal of Physical Anthropology 131: 334-342.

Ossenberg NS. (1977) Congruence of distance matrices based on cranial discrete traits. Cranial measurements, and linguistic-geographic criteria in five Alaskan populations.

Ousley SD (1995) Relationships between Eskimos, Amerindians, and Aleuts: old data, new perspectives. Human Biology. 67(3): 427-458.

Pereira M, Socorro A, Fernandez I, Masleh M, Vidal D, Bianchi NO, Bonatto SL, Salzano FM, and Herrera RJ (2005) Phylogenetic information in polymorphic L1 and Alu insertions from East Asians and Native American populations. Am J Phys Anthropol.

Peterson GM, JI Ward, PI Terasaki, MS Schanfield, RE Ferrell, EM Scott, and MS Parks. (1991) Genetic Polymorphisms in Southwest Alaskan Eskimos. Human Heredity; 41 (4): 236-247.

Relethford JH, FC Lees, and MH Crawford (1980) Population structure and anthropometric variation in rural western Ireland: migration and biological differentiation. Annals of Human Biology. 7(5): 411-28.

Relethford JH (2000) GEOG: Computer Program.

Relethford JH (2003) RMet: Computer Program.

Relethford JH, and Blangero J (1990) Detection of differential gene flow from patterns of quantitative variation. Hum Biol 62:5-25.

Relethford, JH (1996) Genetic drift can obscure population history: problem and solution. Hum Biol 68(1): 29-44.

Relethford JH, Crawford MH, and Blangero J (1997) Genetic drift and gene flow in post-famine Ireland. Hum Biol 69:443-65.

Relethford JH, and Harpending HC (1994) Craniometric variation, genetic theory, and modern human origins. Am J Phys Anthropol 95:249-70.

Relethford JH (2004) Boas and beyond: Migration and craniometric variation. American Journal of Human Biology 16: 379-386

Rohlf, FJ (1998) NTSYSpc: Numerical Taxonomy System, ver. 2.02. Setauket, NY: Exeter Publishing, Ltd.

Ropell AY, SP Davey (1965) Evolution of fur seal management on the Pribilof Islands. Journal of Wildlife Management 29(3): 448-463.

Rubicz R (2001) Origins of the Aleuts: Molecular Perspectives. Unpublished thesis. University of Kansas. Lawrence, Kansas.

Rubicz R, Schurr T, Babb P, and Crawford MH (2003) Mitochondrial DNA and the Origin of the Aleuts. Human Biology 75(6):809-835.

Rubicz, R (2007) Evolutionary consequences of recently founded Aleut communities in the Commander and Pribilof Islands. Unpublished dissertation. Kansas, University of Kansas.

Ruhlen, Merritt (1991) A Guide to the World's Languages, v.1. Stanford University Press: Stanford, California.

Rychkov and Sheremetyeva (1972) Population genetics of the Aleuts of the Commander Islands. Voprosy Anthropologii 40:45-70.

Saillard J, Forster P, Lynnerup N, Bandelt H, and Norby S (2000) mtDNA variation among Greenland Eskimos: The edge of the Beringian expansion. American Journal of Human Genetics 67:718-726.

Saitou N, and Nei M (1987) The neighbor-joining method: a new method for reconstructing phylogenetic trees. Mol Biol Evol 4:406-25.

Salzano FM (2002) Molecular Variability of Amerindians: Widespread but Uneven Information. Annals of Brazilian Academy of Sciences 74:263-243.

Schanfield MS, MH Crawford, JB Dossetor, and H Gershowitz. (1990) Immunoglobulin allotypes in several North American Eskimo populations. Human Biology; 62 (6): 773-789.

Schanfield, Moses S. 1992. Immunoglobulin allotypes (GM and KM) Indicate Multiple founding populations of Native Americans: evidence of at least four migrations to the New World. Human Biology; 64, 3: 381-402.

Scherer AK (2007) Population structure of the Classic period Maya. Am J Phys Anthropol 132:367-80.

Schurr TG (2004) The Peopling of the New World: Perspectives From Molecular Anthropology. Annual Review of Anthropology 33:551-83.

Schurr, Theodore G., RI Sukernik, YB Starikovskaya, and DC Wallace. (1999) Mitochondrial DNA variation in Koryaks and Itel'men: Population replacement in the Okhotsk Sea-Bering Sea region during the Neolithic. American Journal of Physical Anthropology; 108: 1-39.

Sherry TGSaST (2004) Mitochondrial DNA and Y Chromosome Diversity and the Peopling of the Americas: Evolutionary and Demographic Evidence. American Journal of Human Biology 16:420-439.

Sparks CS and RL Jantz (2002) A reassessment of human cranial plasticity: Boas revisited. Proc of the National Academy of Science U.S.A. 99(23):14636-9.

Starikovskaya, YB, RI Sukernik, TG Schurr, AM Kogelnik, and DC Wallace. (1998) mtDNA diversity in Chukcki and Siberian Eskimos: Implications for the genetic history of ancient Beringia and the peopling of the New World.

Szathmary, EJE, NS Ossenberg, MS Clabeaux, DC Cook, MH Crawford, DE Dumond, RL Hall, AB Harper, MG Hurlich, PL Jamison, B Jørgensen, K Korey, M Kowta, R McGhee, C Mielkejohn, TA Murad, CB Pereira, S Pfeiffer, FM Salzano, DS Weaver, SL Zegura, and ML Fleischman (1978) Are the biological differences between North American Indians and Eskimos truly profound? Current Anthropology; 19(4): 673-701.

Torrey B (1983) Slaves of the Harvest. Tanadgusix Corporation, Alaska.

Torroni A, TG Schurr, YB Starikovskaya, MF Cabell, MH Crawford, AG Comuzzie, and DC Wallace (1993a) mtDNA Variation of Aboriginal Siberians Reveals Distinct Genetic Affinities with Native Americans. American Journal of Human Genetics 53:591-608.

Torroni A, TG Schurr, MF Cabell, MD Brown, JV Neel, M Larsen, DG Smith, CM Vullo, and DC Wallace (1993b) Asian Affinities and Continental Radiation of the Four Founding American Native mtDNAs. American Journal of Human Genetics 53:563-590.

Weinelt, Martin (1996) Online Mapping Creation. Computer Program <http://www.aquarius.geomar.de/omc_intro.html> Accessed: November 27, 2007.

Williams-Blangero S, and Blangero J (1989) Anthropometric variation and the genetic structure of the Jirels of Nepal. Hum Biol 61:1-12.

Zlojutro, M, RC Rubicz, EJ Devor, VA Spisyn, SV Makarov, K Wilson, and MH Crawford. (2006) Genetic structure of the Aleuts and circumpolar populations based on mitochondrial DNA sequences: A synthesis. American Journal of Physical Anthropology; 129: 446-464.

Males Within-group Phenotypic Variance				
Mean = 0.939				
Population	**r(ii)**	**Observed**	**Expected**	**Residual**
St. Paul	0.017028	1.016	0.933	0.083
St. George	0.023836	1.034	0.926	0.108
Savoonga	0.009245	0.922	0.940	-0.018
Gambell	0.00	0.838	0.949	-0.111

Appendix A. Estimates of within-group phenotypic variance, distance from the average centroid and deviations from expectation of phenotypic variance using the Relethford-Blangero method on the four twelve original variables on males.

Females Within-group Phenotypic Variance				
Mean = 0.928				
Population	**r(ii)**	**Observed**	**Expected**	**Residual**
St. Paul	0.026936	1.020	0.919	0.102
St. George	0.016555	1.192	0.928	0.264
Gambell	0.002988	0.776	0.941	-0.165
Savoonga	0.018873	0.883	0.926	-0.043

Appendix B. Estimates of within-group phenotypic variance, distance from the average centroid and deviations from expectation of phenotypic variance using the Relethford-Blangero method on the four twelve original variables for females.